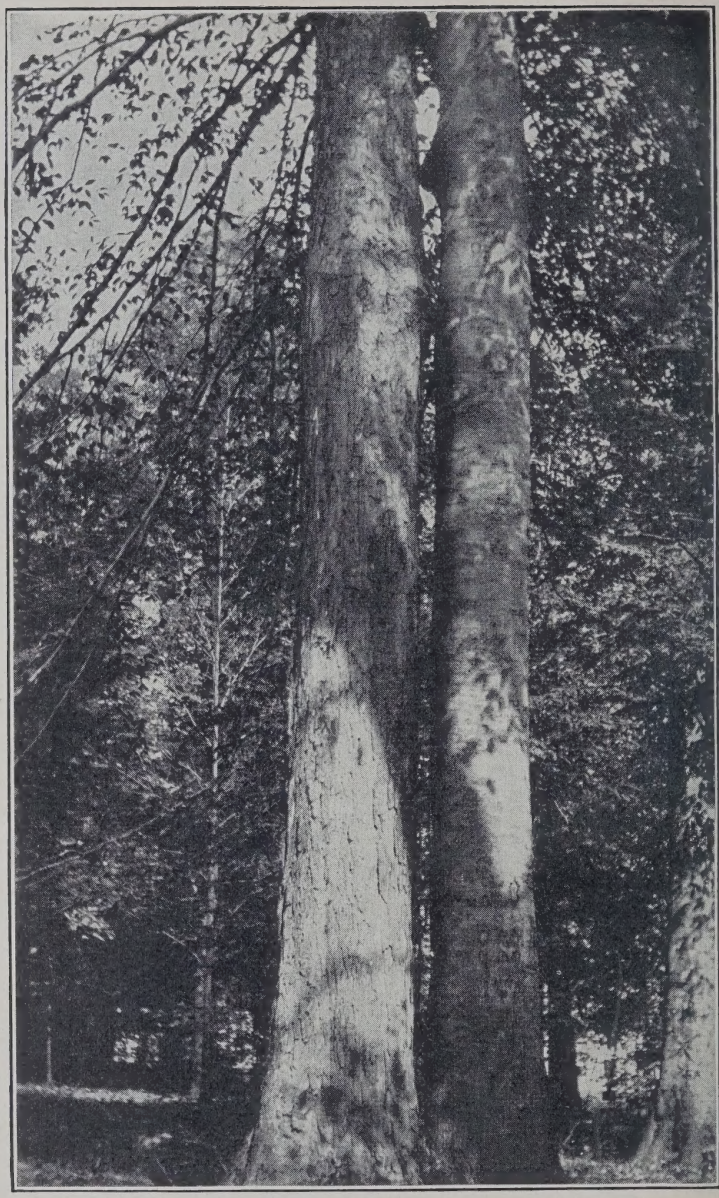
Digitized by the Internet Archive
in 2026 with funding from
University of Toronto

https://archive.org/details/textbookofbotany00mott

A TEXTBOOK OF BOTANY FOR COLLEGE STUDENTS



Two Veterans of a Beech-Maple Climax, Campus, Indiana University. Photograph by Glenn W. Blaydes.

FRONTISPIECE

A TEXTBOOK OF BOTANY FOR COLLEGE STUDENTS

Being a Revision and Amplification
of "A College Textbook of Botany
for First Year Students"

BY

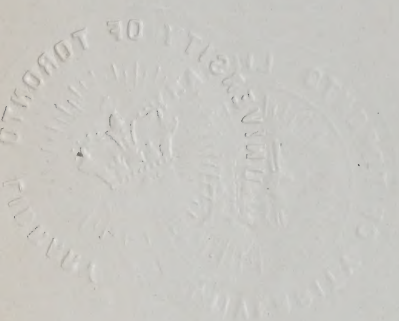
DAVID MYERS MOTTIER

PROFESSOR OF BOTANY AND HEAD OF THE DEPARTMENT IN
INDIANA UNIVERSITY

WITH 542 ILLUSTRATIONS

281725
1. 33
20

PHILADELPHIA
P. BLAKISTON'S SON & CO., INC.
1012 WALNUT STREET



COPYRIGHT, 1932, BY P. BLAKISTON'S SON & CO., INC.

PRINTED IN U. S. A.
BY THE MAPLE PRESS COMPANY, YORK, PA.

PREFACE

After many years of experience in teaching elementary botany in the university, the author is convinced that the beginner who has any taste for the subject, or in whom a desire to know something of plant life may be stimulated, has, first of all, an interest in a knowledge of living individual plants, as manifested in their form, structure, function, reproduction, and adjustment to the places in which they live.

Since the student usually associates his knowledge of structure, function, and life history with some definite plant or some part of a plant, the author has endeavored not only to present the subject-matter in concrete form, but to include, where possible, the material used in the observation, or in the specific type for life history study.

In the preparation and arrangement of materials, both in the shorter course edition, and in this enlarged edition, the author has been guided by pedagogical principles acquired through long experience and not by the desire to make an elementary scientific treatise. Whenever feasible, the human interest side of the subject has been referred to or briefly discussed.

In this amplified edition the writer, following the valuable suggestions of those who used the shorter course edition, and his own experience, has rearranged certain matters; enlarged other parts; and added new chapters. The sections dealing with seed and fruit and pollination have been extended and more fully illustrated. The new material includes a chapter on geographic distribution, and a brief chapter on heredity and Mendel's law. A summary concludes the presentation of each of the several great groups of plants, and at the close of each chapter, a list of topics for review and discussion has been added. A notable feature is the addition of many illustrations, those from Strasburger's "Textbook of Botany" having been made available by the courtesy of the publishers, The Macmillan Co., New York.

The fundamental idea of the shorter course edition has been maintained in this edition, namely, the presentation of the data from the standpoint of the plant as a concrete illustration of the phenomena discussed.

The author takes pleasure in acknowledging his obligation to his colleague, Professor James M. Van Hook for suggestions and for his kindness in reading both manuscript and proof. To his colleague Professor F. M. Andrews, for reading the proof and for timely suggestions, and to all others who have offered friendly criticisms and have made helpful suggestions, the author also expresses his appreciation of their courtesy and helpfulness.

DAVID M. MOTTIER.

INDIANA UNIVERSITY,

CONTENTS

PAGE

PREFACE v

INTRODUCTION ix

CHAPTER I

THE LIFE OF A SEED-BEARING PLANT 1

CHAPTER II

THE CELL, THE UNIT OF STRUCTURE AND FUNCTION 7

CHAPTER III

THE LEAF 31

CHAPTER IV

THE STEM 77

CHAPTER V

THE ROOT 126

CHAPTER VI

MOVEMENT OF WATER AND FOOD IN PLANTS 157

CHAPTER VII

SEEDS AND SEEDLINGS 163

CHAPTER VIII

UTILIZATION OF FOOD—ENERGY RELEASE 171

CHAPTER IX

GROWTH AND RESPONSE TO STIMULI 177

CHAPTER X

THALLOPHYTA—MYXOMYCETES, SCHIZOPHYTA 186

CHAPTER XI

THALLOPHYTA—ZYGOPHYCEAE 206

CHAPTER XII

THALLOPHYTA—CHLOROPHYCEAE—GREEN ALGAE 224

PAGE

CHAPTER XIII
THALLOPHYTA—PHAEOPHYCEAE—BROWN ALGAE 259

CHAPTER XIV
THALLOPHYTA—RHODOPHYCEAE—RED ALGAE 271

CHAPTER XV
THALLOPHYTA—FUNGI 282

CHAPTER XVI
BRYOPHYTA 336

CHAPTER XVII
PTERIDOPHYTA 383

CHAPTER XVIII
SPERMATOPHYTA—GYMNOSPERMS 428

CHAPTER XIX
SPERMATOPHYTA—ANGIOSPERMS 470

CHAPTER XX
DISPERSAL OF SEEDS AND FRUITS 529

CHAPTER XXI
GEOGRAPHIC DISTRIBUTION OF PLANTS 540

CHAPTER XXII
HEREDITY 581

INDEX 589

INTRODUCTION

THE BIOLOGICAL SCIENCES

All living organisms known to science may be placed in either one or the other of two great sub-divisions, or kingdoms, namely, plants and animals.

All those sciences dealing with plants and plant life as it now exists constitute the subject of Botany, and those pertaining to animals, the subject of Zoölogy. Each of these two great subjects comprises many subdivisions, some of which, like Bacteriology, Human Physiology, and the more recently segregated subject, Genetics, are often regarded as separate sciences. All the sciences dealing with living organisms constitute, therefore, the subject of Biology. The biological sciences now generally recognized as such are: Botany, Bacteriology, Human Physiology, Zoölogy, Medical Science and Genetics. The subject of Genetics as applied to plant life pertains to the experimental study of heredity.

THE PLANT KINGDOM

Spermatophyta

The most conspicuous plants which one sees in the park, field, and garden are trees, bushes, field crops, garden vegetables, and the ornamental flowers of garden and woodland. All of these plants produce seeds, and all bear spores. Because they bear seeds they have been named *Spermatophyta*. They are known also botanically as the "flowering plants." Plants cannot produce seeds without first developing flowers, and flowers are spore-bearers as well as seed producers. The relation of these two functions will be pointed out in subsequent pages.

Pteridophyta

In woodland and in conservatory one finds ferns, and fernlike plants, such as horsetails and club mosses. Like seed-bearing plants they possess roots, stems, and leaves; unlike seed plants they do not bear seeds but merely spores. They are the *Pteridophyta*.

Bryophyta

No woodland or open field is lacking in the ever present mosses which are so common upon tree trunks, old logs, rocks, and upon moist shady soil,

or upon the moist shady surfaces of old buildings and walls. Less abundant and more restricted in distribution are the liverworts, a group of plants related to the mosses. Liverworts and mosses make up the *Bryophyta.*

Algae

Upon moist earth, tree trunks, and stones, we see green and blue-green films; in ponds, lakes, and streams, green threads and scums; in bodies of salt water, sea weeds, green, brown, and red. All of these are the *Algae.*

Fungi

The smuts, rusts, and mildews, so common and destructive to field crops and garden plants, together with moulds and mushrooms constitute the *Fungi.* Plants commonly known as Lichens represent, with few exceptions, a combination of a fungus and an alga.

Bacteria

Bacteria are extremely minute microscopic plants, appearing colorless as individuals, and popularly known as "germs" or "microbes." They are the smallest of all known living things. Certain bacteria are injurious to man, causing such diseases as typhoid fever, scarlet fever, diphtheria, tetanus or lockjaw, etc. Many, on the contrary, are benefactors of the human race, because they play a necessary role in processes leading to the fertility of the soil. Many bacteria act also as scavengers in causing the decay of dead organisms. They are nature's sanitary agents. Bacteria are more like fungi than algae since they do not make their food.

Algae, fungi, lichens and bacteria are often referred to as the *Thallophyta.*

Slime Moulds

There is still another group of low plants representing the border line between plants and animals. They reveal distinct animal as well as plant characteristics. They grow upon decaying logs, stumps, in rich garden earth or upon the lawn, and sometimes upon old apple pomace. One species is a parasite upon such plants as the cabbage. These wonderful organisms are the Slime Moulds, or the *Myxomycetes*, which means slime fungi.

All the sciences dealing directly with any or all of the above named groups of plants constitute the subject of *Botany.* On the other hand, all the sciences which are concerned directly with animals make up the subject of *Zoölogy*, although the study of medicine and human anatomy

and physiology are regarded as separate sciences; they are not usually included under Zoölogy.

All plants and animals have one thing in common—they are made of the same kind of structural units, namely, cells. The smallest and simplest living things known, bacteria and amoebae, consist each of one cell. The largest living things, the giant Sequoias and Eucalyptus trees, are made up of many millions of cells which, however, have developed from one cell, the egg, in a definite and orderly manner.

A TEXTBOOK OF BOTANY

FOR

COLLEGE STUDENTS

CHAPTER I

THE LIFE OF A SEED-BEARING PLANT

In taking up the study of plant life as an organized science it will be useful to make a beginning by learning to know more accurately some of the obvious characteristics of some common plant, which are known very inaccurately, and to think clearly and scientifically about these obvious features instead of thinking vaguely and unscientifically. Any common and well known plant, such as a bean or a small shade tree, will serve as an illustration.

Let us start with the seedlings about a week old or older. The seedling of a bean will be suitable inasmuch as a specimen may be easily grown and kept conveniently at hand. A picture of such a seedling is seen in Fig. 1. In the seedling we see at once that it has an axis, the lower end of which growing downward into the ground is the first, or *primary root*, while the upper end of the axis which grows straight upward is the *shoot*. The two thick fleshy seed leaves are the *cotyledons*. That part of the shoot between root and cotyledons is the *hypocotyl*. The axis above the cotyledons is the *epicotyl*. The epicotyl will develop into the stem. The stem bears a pair of leaves, the first foliage leaves. The tip of this stem ends in a tiny bud. A bud is the end of a stem or of a stem branch covered by small leaves of some sort. The leaves of a bud may be young foliage leaves, scale-like leaves, or the parts of a flower, as in a flower bud.

The first pair of foliage leaves of the common bean is different from the leaves which develop later. They have but one blade each, and may be known as *juvenile* leaves, or the leaves of the young plant. The leaves which develop upon the stem following the first pair possess more than one blade each. How many? They may be found upon a seedling two

or three weeks old. These leaves with more than one blade are called the adult leaves, because they are like those which will appear on the adult, or grown up plant. Like the seedling of the common bean, many young forest trees (box elder, oak, walnut) bear juvenile leaves which are unlike the adult leaves.

The Adult Plant.—We may now turn our attention to a larger shade tree, or to the picture in Fig. 2 which is a simplified diagram of a larger plant including the cotyledons. As the seedling grows into the larger tree we find that the primary root becomes thicker and longer, developing

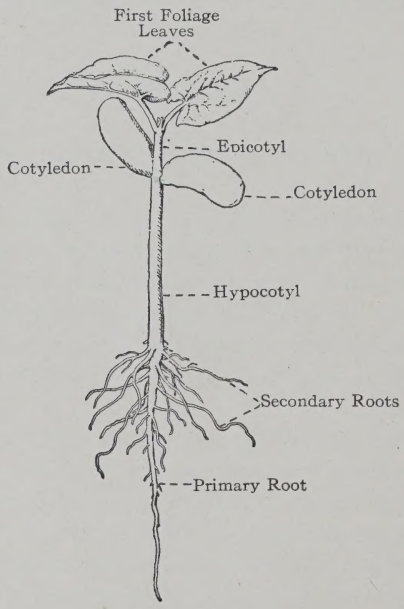


FIG. 1.—Seedling of Lima bean.

many side roots or root branches. With age these side roots branch and re-branch many times, so that the adult tree has a great root system with about as many large and small roots as there are large and small branches upon the stem or trunk.

The roots which spring from the primary root or its branches are *secondary* roots. Roots which arise from any other part of the plant, such as leaves or stems, are known as *adventitious* roots. In Indian corn and in other grasses the primary root and its branches die after a short time, and the roots of the adult plants are all adventitious roots.

Fibrous roots are slender thread-like roots developed as branches from the primary root or as adventitious roots. The roots of grasses are chiefly fibrous roots.

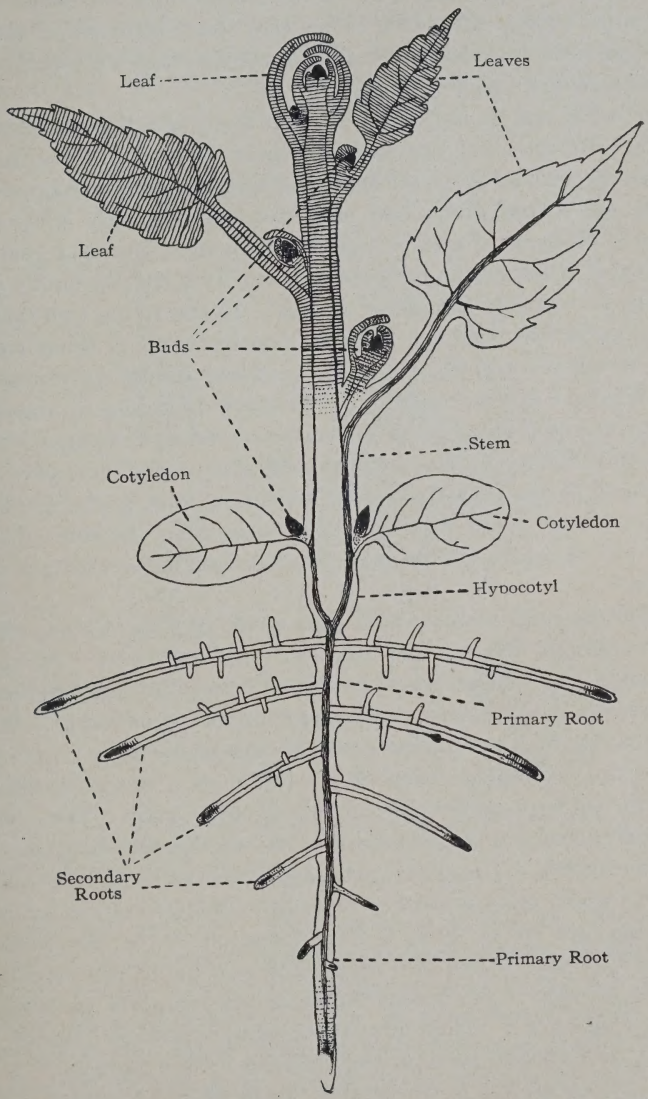


FIG. 2.—Diagram of a longitudinal section of a young dicotylous plant.

Keeping in mind our shade tree, we observe that the stem becomes the trunk. The trunk of a pine tree, for example, is a straight shaft extending

from the ground to the top. In many trees the main stem or trunk is lost in two or more large branches, as seen in elms, maples, and in others. Stem branches arise from buds which are developed in the axils of the leaves (Fig. 2). The axil of a leaf is the angular space between the stem and the upper surface of the base of the leaf. Each stem ends in a terminal bud. Buds which develop in the axils of the cotyledons are often referred to as cotyledonary buds.

In the adult tree we notice further that many of the branches are long, extending from the trunk out to the limits of the spread of the tree, while others are shorter and fill in the spaces between the longer branches. Did you ever see a tree which had only the long branches without short branches to fill in the spaces between? If so, what kind of a tree was it?

The trunk, branches and old roots of our trees consist mainly of wood covered by a relatively thin layer of bark. In the young tree the bark is usually smooth, but with age it cracks and scales off or sloughs off. Of the trees which you know, can you recognize any by the appearance of the bark? What are evergreen plants? What are deciduous trees or bushes? As a rule what kind of leaves have deciduous trees as compared with evergreens in cold climates? Have you any explanation for these phenomena?

The roots of the plant have two main functions, anchorage and the absorption of water and dissolved substances from the soil. The stem develops leaves (which are the great primary food makers), roots, flowers, and fruits.

The Flower.—All plants which bear seeds and fruits must first bear flowers, for flowers are the forerunners of seeds and fruits. Flowers also produce spores as well as seeds, and it will be extremely interesting to learn about the part taken by the spores in seed production. We may become familiar with a complete flower by examining some large blossom in connection with the pictures shown in Figure 3, which represents the flower of the common garden Nasturtium (Tropaeolum). The outer part of this flower consists of a circle of five *sepals* on the outside followed by a circle of five *petals*. The petals are larger than the sepals. The sepals form a spur which bears a nectary in its tip. Nectar is collected by bees and changed into honey which is then deposited by the bees in the cells of the honeycomb. When two sepals and two petals are carefully cut away from one side of the flower, the spore-bearing parts are revealed in the center (Fig. 3, A). These are the *stamens*, several in number, and a *pistil*, C, a flask-shaped structure surrounded by the stamens. A single stamen is shown at B. It consists of the terminal thickened part, the *anther*, and the slender stalk, the *filament*. Figure 3, C is an enlarged drawing of the pistil which consists of three parts, as seen from the outside, the *ovulary* and the *style* with its three cleft *stigma* at the top. The

ovulary contains the *ovules* which are young and immature seeds. The ovules are revealed in a cross section of the ovulary shown in Figure 3, D.

The Formation of Seed and Fruit.—The Nasturtium flower bears two kinds of spores. One kind is called *pollen* which is produced in the anthers. Pollen spores are minute, appearing in bulk to the naked eye as colored dust. The other kind of spores are the *large* spores which are developed inside the ovule. Without the functioning of these two kinds of spores

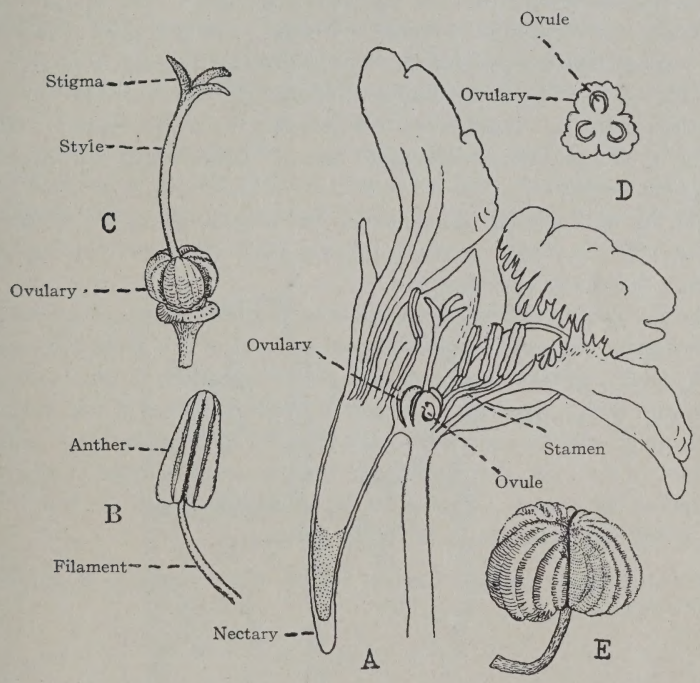


FIG. 3.—Flower and fruit of the garden Nasturtium (*Tropaeolum*). A, side view of flower after removal of two sepals and two petals; B, stamen; C, pistil; D, cross section of ovulary; E, fruit.

seeds could not develop.* The process is as follows: the *large spore* inside the ovule produces eventually a germ cell, the *egg*. When the pollen spore is placed upon the stigma a very delicate and slender tube grows from it. This tube is called the *pollen tube*. It grows from the pollen spore on the stigma down through stigma and style into the ovulary where its tip end enters an ovule through an opening in the end of the latter until the egg is reached. In the tip of the tube there are two germ cells called *sperms*.

* There are some exceptions. The common dandelion is one; it produces seeds without the functioning of pollen.

The tube opens when it reaches the egg and one sperm* unites with the egg. The fecundated egg now develops into an embryo plant, in this case an embryo Nasturtium. The young ovule now gradually enlarges and matures into the seed. By the time the seed is ripe the embryo plant in it is quite large. In very large seeds like those of the Lima bean the embryo is very large, having an axis, two large cotyledons and a bud of two tiny foliage leaves.

The fruit develops from the wall of the ovulary. The mature fruit of the Nasturtium resembles somewhat a small, rounded peanut in appearance. When ripe it separates into two or three parts, each bearing a single seed (Fig. 3, E). In some plants the fruits develop without seeds as in the seedless fruits. How many seedless fruits do you know? What is the difference between seedless and "seeded" fruits which one buys at the grocery or market?

The life of the plant is continued in the embryo of the seed. In a seedless fruit the ovulary matures into the fruit while the ovules shrivel up and may disappear completely.

The foregoing is a very brief story of the life history of a seed plant. In subsequent chapters a more detailed account of the plant will be given, dealing with the structure, function and adaptation of leaf, stem, root, flower, and fruit. Inasmuch as each of these members of the plant body is made up of cells, and as the function of each part represents the combined functions of its cells, it is important that some knowledge of the cell be acquired at the outset. The next chapter will deal with the cell, the unit of structure and function in all living things.

* The other sperm does not function save in certain plants to be mentioned in another chapter.

CHAPTER II

THE CELL, THE UNIT OF STRUCTURE AND FUNCTION

General Description.—A general idea of a typical plant cell may be obtained by direct observation of a leaf of the small, seed-bearing aquatic plant, Elodea, or of the moss, Funaria, or some other suitable plant.

Viewed from the surface with the microscope, the cells of the leaf of Elodea, except at the margins, appear generally rectangular in outline, as shown in Figure 4. At the first glance, the most conspicuous thing seen is the green color, due to numerous rounded green bodies, the *chloroplasts*,

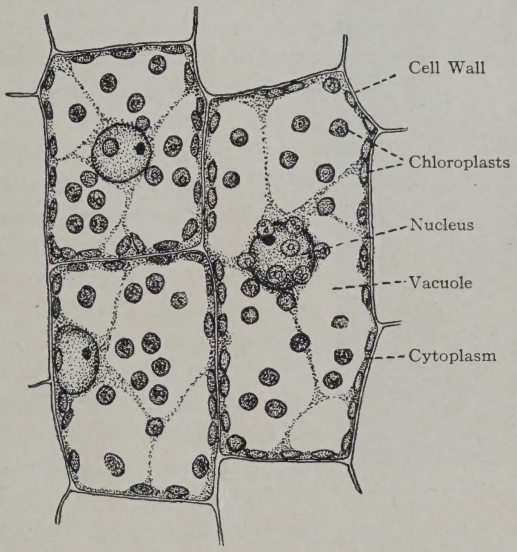


FIG. 4.—Three cells from leaf of Elodea.

which may be somewhat evenly distributed in the cell, or aggregated in masses. Each cell has a thin, colorless wall. With the exception of the midrib, the leaf is only one cell in thickness, and it must be remembered that each cell appearing four-sided in outline, is not flat like a sheet of paper, but in the form of a box with six sides.

Spread over the entire interior surface of each cell wall is a very thin, colorless layer of living substance, the *cytoplasm*, in which are held or

embedded the conspicuous chloroplasts. At some point in this cytoplasmic layer is a more refractive, or grayish, rounded body, the *nucleus*. In the live cell the nucleus is not conspicuous, and may not be readily observed.

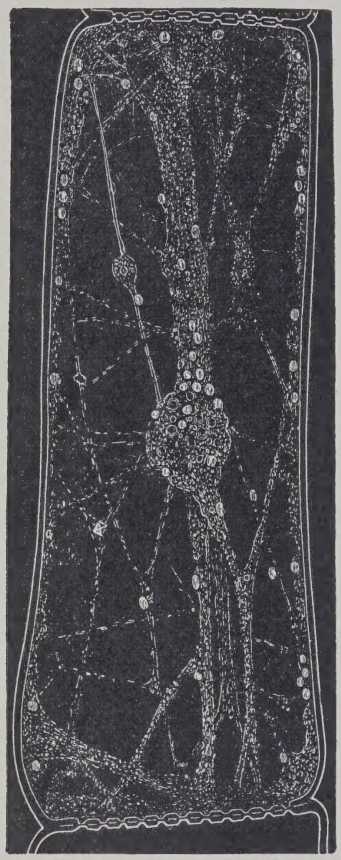


FIG. 5.—Appearance of a hair-cell from the bud of a gourd plant projected against a black background. The rounded objects in lighter color are plastids. A small crystal is seen at the left. A thick cytoplasmic strand extends lengthwise through the cell; the enlarged rounded part contains the nucleus. Numerous fine threads traverse the vacuole. (From Sachs' "Lectures on the Physiology of Plants" Clarendon Press.)

In the central part of the cell in question is a large cavity, constituting the larger part of the volume of the cell, the *vacuole*, which is filled with a watery fluid, the *cell sap*. In some cells strands of cytoplasm traverse the vacuole, and upon them chloroplasts may be located.

Movement of the Cytoplasm in the Cell.—In certain cells a striking feature is the movement of the chloroplasts, which may be seen to pass down one side of the cell, across the end, and return along the opposite side and end, thus making a complete rotation. The movement of the chloroplasts is due to the motion of the innermost layer of cytoplasm, i.e., that next to the vacuole, the chloroplasts being carried along with the moving cytoplasm. Visible cytoplasmic movement is a conspicuous phenomenon in many adult cells. In certain cells, as those of the stamen hairs of the spider-wort, Tradescantia, the movement takes place in different directions in different parts of the same cell, thus constituting a sort of circulatory, instead of a rotary movement. A fine illustration is seen also in the cells of the hairs of the gourd plant. Figure 5 is an illustration of such a cell shown against a dark background. In the large and small strands and threads traversing the vacuole an active *streaming* goes on continually and in different directions, i.e., in some strands from the lower towards the upper end of the cell; in others in the reverse direction, and in some strands the movement is up on one side of the strand and down on the opposite side. The *plastids*, the rounded lighter bodies, may be carried along in the streaming cytoplasm.

Fixed and Stained Cells.—We shall now consider cells from the tip of some growing organ such as a root or stem, which has been properly killed (fixed), sectioned and stained, in order to learn more in detail of their internal structure. In a young cell we find that the cavity is completely filled with cytoplasm, near the center of which lies the conspicuous nucleus (Fig. 6, A). In the cytoplasm are also numerous very small, rounded and rod-shaped bodies. Some of these bodies are the beginnings (primordia) of structures known as plastids, such as chloroplasts and *leucoplasts*, to be described more fully in subsequent para-

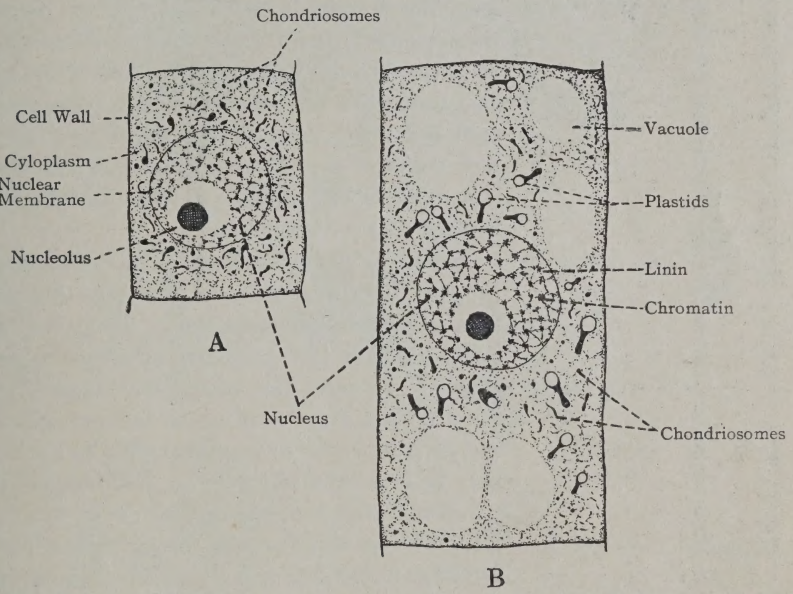


FIG. 6.—Sections of fixed and stained cells from the root tip of the garden pea (*Pisum sativum*). A, young cell before appearance of vacuoles. B, older cell with vacuoles.

graphs; others, the more minute, whose function is unknown, will be called *chondriosomes* (mitochondria).

As the cells become older and increase in size before reaching the adult stage, the quantity of cytoplasm may not increase in proportion to the volume of the cell. The increase in size is due largely to the absorption of water, which accumulates in one or more vacuoles. The result is similar to that seen in the leaf of Elodea, or as shown in Figure 4. In older cells the cytoplasm becomes spread over the inner surface of the cell wall, while one or more vacuoles occupy the bulk of the cell cavity, as in the cells of the leaf of Elodea, or as shown in Figure 7. This thin layer of cytoplasm spread over the inner surface of the cell wall is spoken of in the older literature as the *primordial utricle*.

It should be borne in mind that it is not the entire cytoplasmic layer that is in perceptible motion, but merely the inner, and more fluid part next to the vacuole. The cytoplasm lying nearest the cell wall, and in contact with it, is stationary. The exceedingly thin surface layer next to the cell wall, which constitutes the outer surface of the cytoplasm, is the *plasma membrane*. The plasma membrane is exceedingly thin, colorless, homogeneous, and of a much firmer consistency than the rest of the cytoplasm. It is now regarded as the more sensitive part of the cell, i.e., it is the part which responds to stimuli, and which tends to regulate the permeability of the cell to various substances.

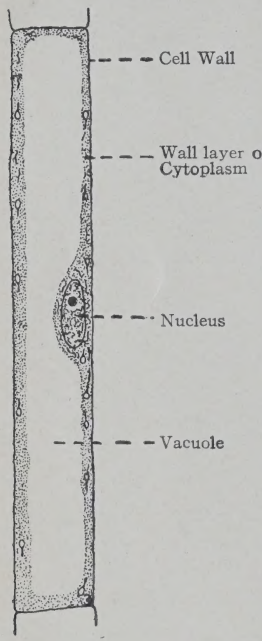


FIG. 7.—Cell which has elongated through growth by hydration. Note the large vacuole and the thin layer of cytoplasm along the wall.

From the foregoing we may now define a cell as a nucleated mass of cytoplasm having a common and continuous plasma membrane. A cell may contain two or more nuclei, in which case it is a multinucleated cell. A multinucleated cell is often called a *coenocyte*.

Structure of the Nucleus.—Turning our attention now to the nucleus, we find that this structure is generally a spherical or elongated body delimited from the cytoplasm by a definite membrane of its own, the *nuclear membrane* (Fig. 6, A). Within may be seen one or more globular bodies, the *nucleolus* or *nucleoli*. The nucleolus may lie in a definitely circumscribed area. Distributed throughout the nuclear cavity is a mesh work of very fine threads, the *linin*, upon which are held numerous irregular granules varying in size, the *chromatin granules*. The *chromatin* is readily stained by various specific stains, while the linin tends to remain colorless. The rest of the nuclear cavity is occupied by a watery fluid, the nuclear sap (karyolymph).

Plastids.—Certain bodies present in the cytoplasm of the cell, which are centers of chemical activity and concerned with the building up of chemical compounds, are known as plastids. They are *chloroplasts*, *leucoplasts*, *chromoplasts* (*chromatophores*), *protein plastids*, and *oil plastids*.

Chloroplasts.—Of the plastids in the cell, the most conspicuous, and probably the most important, are the *chloroplasts*, which contain the green pigment, *chlorophyll*, and which build up starch by the process of photosynthesis. Because of this fact, the starch formed in the chloroplast is called photosynthetic starch.

In the higher plants chloroplasts are usually small, globular, oval, elongated, or polygonal if crowded; but in some of the algae (pond silks) they are larger in proportion to the size of the cell, and few in number, and of various shapes, such as tabular, spiral, cylindrical, cup-shaped, or

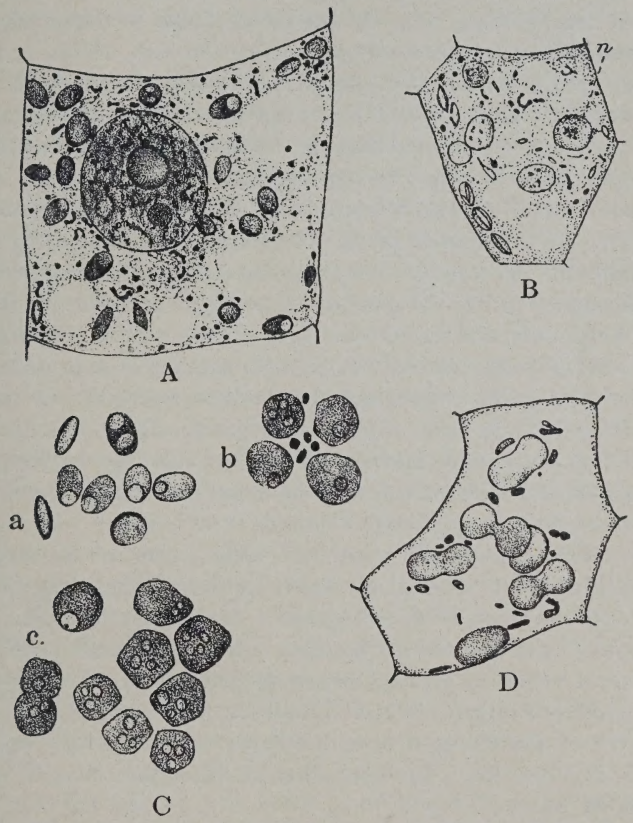


FIG. 8.—Development of chloroplasts from primordia. A, cell from hypocotyl of embryo of the pine (*Pinus Banksiana*) with young chloroplasts and very small, round, and rod-shaped bodies. B, cell of meristematic tissue of the liverwort (*Marchantia*) with chloroplasts in different stages of development. C, developmental stages of chloroplasts in young seedling of Pinus. D, older cell of Marchantia in which fully developed chloroplasts are dividing.

star-shaped. Each chloroplast may contain one or more starch inclusions (Fig. 8, C).

Structurally the chloroplast consists of a firmer framework, the *stroma*, which contains the pigment, chlorophyll. The center of the stroma is less dense, or somewhat vacuole-like, while the firmer periphery is porous. The pigment is held in the porous peripheral portion.

In embryonic cells, and in young meristem, chloroplasts, and other plastids as well, arise from very minute, granular, or rod-shaped beginnings termed *primordia*. The rod-like primordia are either straight, curved, or comma-like, or club-shaped (Fig. 8, A, B, D). There is much evidence to support the belief that the primordia divide by fission, and that they are permanent organs of the cell. In the development of the chloroplasts in meristematic tissue the primordium increases in size, becoming rounded, lenticular, or sometimes club-shaped. The less dense center can be readily seen in stained cells. In it the starch inclusion accumulates. Fig. 8, C, *a*, *b*, *c*, shows several steps in the development of the chloroplast from the primordia in a very young seedling of the pine.

The adult, or full grown, chloroplast is capable of division by constriction (Fig. 8, D). In this respect adult chloroplasts differ from other plastids.

Chlorophyll.—As stated in the foregoing paragraph, the green color of the chloroplasts is due to the presence of the pigment, chlorophyll. A few simple experiments will throw some light on the nature of this pigment. If some fresh leaves that are not too old, or a quantity of some suitable alga, are first steeped in hot water, and then, after draining off the water, are kept in alcohol for an hour or longer, the green color will be dissolved in the alcohol, and the plant material will be left colorless. If the cells are now examined with the microscope, the stroma of the chloroplast will be seen as before treatment, though colorless.

An alcoholic extract of chlorophyll, when observed by transmitted light in a test tube or other glass vessel, appears a clear, deep green. In reflected light, as when examined against a dark background, it appears a dark purple, due to a sort of fluorescence. If the extract be kept in a cool, dark place, the chlorophyll may remain unchanged for a few days, but, if exposed to direct sunlight for a few minutes, it will be quickly decomposed, as indicated by the disappearance of the green color and the appearance of a dark, smoky color. The instability of chlorophyll may be shown in various other ways.

That the chlorophyll in the alcoholic extract contains different pigments may readily be demonstrated by diluting a small quantity with water and adding benzol. In a short time the benzol rises to the surface of the mixture as a sharply defined, deep green layer, while the alcohol and water below will be of a pale straw color. The green pigment at the top is chlorophyll green, and the yellowish pigment below is chlorophyll yellow. The latter is composed of two pigments, the orange-colored *carotin*, and the lemon-yellow *xanthophyll*. Chlorophyll green is composed of two pigments, *chlorophyll a*, which is a deep, blue-green, and *chlorophyll b*, a lighter green. Chlorophyll is composed of carbon, oxygen, hydrogen, nitrogen, and one metal, magnesium.

If growing plants are kept in the dark, the chloroplasts will appear yellowish, owing to lack of chlorophyll green. The yellow pigment, under this circumstance, is spoken of as *etiolin*. Barring some exceptions, light, therefore, is necessary to the development of chlorophyll. In the seeds of the pine, and of some other plants, the chloroplasts become green in darkness, or with the aid of whatever light that may penetrate the seed coat.

Other Pigments in Plastids.—In certain groups of plants other pigments occur in the plastids along with chlorophyll, modifying the green color or obscuring it completely. In many of the blue-green algae the additional pigment is *phycocyanin*, which imparts the bluish color to the cells, while in the red algae the additional red pigment is known as *phycoerythrin*. When the plants are killed these two pigments are soluble in water and present a characteristic fluorescence in reflected light. The brown color in the brown algae (Phaeophyceae) has been attributed to the additional brown pigment, *phycophaein*. There is some difference of opinion as to the presence of chlorophyll in the brown algae, it being maintained that only one pigment, *fucoxanthin*, is present, which is closely related to chlorophyll. The characteristic color of the chloroplast in Diatoms is held by some authors to be similar to that in the brown algae, while others regard it as partaking of the nature of carotin. The name, *diatomin*, has also been applied to it.

Pigments Dissolved in the Cell Sap.—Pigments, chiefly blues and reds, occur in the cell sap of various plants, imparting those colors to the parts containing the pigments. They are known as *anthocyan*, or *anthocyanin*. Thus the red color of a rose or the blue color of a violet is due to anthocyanin. The yellow pigment, xanthophyll, occurs in the petals of some flowers, as the yellow tulip. This pigment is regarded as being produced by numerous small, round, or rod-shaped plastids, each plastid forming a tiny droplet of yellow fluid. The droplets finally run together and collect in the cell sap. It is not at all improbable that anthocyanin is a product of definite living plastids, rather than a chemical combination produced in the cell sap as a mother fluid.

Leucoplasts.—In certain parts of plants, are found colorless plastids that build up starch also (Fig. 10, A, B). This starch is known as storage starch, inasmuch as it is stored food and as it is made from the starch or other carbon compounds originally manufactured in the chloroplasts. An illustration will serve to make this statement clear. In the leaves of the potato plant, for example, starch is made by the chloroplasts. This is photosynthetic starch. This is changed to a form of sugar (glucose) and transported from the leaves, through the stem, to the tuber under the ground. The leucoplasts in the cells of the tuber change the glucose into

starch. The changing of glucose into starch by the leucoplast does not require light as a source of energy.

Origin of Leucoplasts.—Leucoplasts, like chloroplasts, are derived, in embryonic cells, from small, granular or rod-like primordia, as shown in Fig. 6 and in Fig. 9, A, B. In the transformation of the leucoplast from the rod-shaped primordium in the root of the common pea, this body

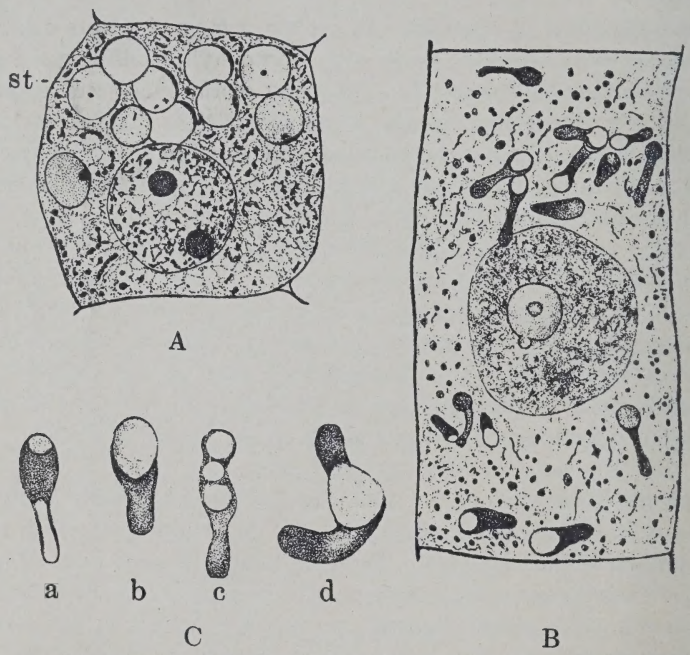


FIG. 9.—Development of leucoplasts in the root tip of the garden pea (*Pisum sativum*). A, cell from root cap with several starch grains *st*, in which the plastid appears as a dark, narrow crescent at one side of the colorless starch grain; the larger straight or curved, rod-shaped bodies are probably plastid primordia, and the very small round granules are regarded as chondriosomes. B, cell from meristem of root with leucoplasts in different stages of development. C, *a*, *b*, *c*, *d*, leucoplasts with starch inclusions, three inclusions being present in *c*.

increases in size, and, either near one end or in the middle, an enlargement appears containing a substance giving a starch reaction (Fig. 9, B). Two or more starch inclusions may be formed in a developing primordium, as in Fig. 9, C. In cells of the root cap, each leucoplast contains a relatively large starch grain, the plastid covering the starch as an extremely thin layer, thickened, however, in the form of a crescent at one side (Fig. 9, A, *st*).

Similarity of Chloroplasts and Leucoplasts.—Chloroplasts and leucoplasts are morphologically alike; that is, (1) they originate from primordia

that cannot be distinguished from one another in young cells; and (2) when exposed to the light, leucoplasts may develop chlorophyll and

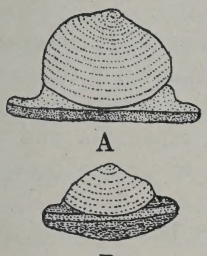


FIG. 10.—Leucoplasts with starch grains from surface of tuber of *Phajus grandifolius*, an orchid. B, the plastid has become green, illustrating the change from leucoplast to chloroplast. (Strasburger, Macmillan Co.)

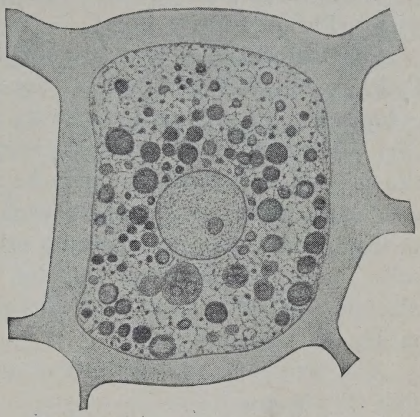


FIG. 11.—Cell of the aleurone layer of a grain of corn, showing the aleurone granules in all stages of development from the primorida.

become green (Fig. 10). This fact can be demonstrated by exposing young growing potato tubers to the light. In the outer parts the leucoplasts will become green. It happens also that chloroplasts, in certain parts of the plant, may function as leucoplasts, as in the cells at the base of the leaf of Elodea.

FIG. 12.—Cell from the sepal of the Nasturtium with numerous angular chromoplasts (chromatophores).

Chloroplasts, however, can multiply by division in the mature, or adult stage, while leucoplasts cannot do so when mature. The activity of leucoplasts is confined chiefly, though not exclusively, to older cells that have passed into a permanent vegetative condition.

Protein Plastids and Other Plastids.—Protein plastids may be readily observed in the outer, or aleurone, layer of the endosperm of certain seeds, such as those of Indian corn. Here they are seen in the form of conspicuous globules, which may be colorless or variously colored, as in the corn with blue endosperm (Fig. 11). They arise from small primordia.

The oil in the seed of the castor oil plant (Ricinus) is derived, presumably, from oil plastids. These may be morphologically similar to leucoplasts.

Chromoplasts.—Chromoplasts are definite bodies occurring in many cells containing certain pigments. A good example is seen in the sepals of the common garden Nasturtium (Tropaeolum) or in the root of the carrot (Fig. 12).

Cell Inclusions.—The substances built up by plastids, such as carbohydrates, oils, fats, and proteins, are often referred to as inclusions of the cytoplasm. In addition to these are mineral crystals of various composition. They are very abundant in stems and in leaves of many plants. In the cell sap of the vacuoles may be found various inorganic salts, especially nitrates, sulphates, and phosphates. Organic acids, such as malic, tartaric, and oxalic, together with salts of these are often found in plant cells. Glycogen, mucilage, amides, especially asparagin, and various alkaloids and glucosides occur in the cell sap, where anthocyanin pigments also accumulate.

The structure and contents of the cell may be summarized in the following diagram:

- Cell
  - Cell wall
  - Protoplast
    - Nucleus
      - Nuclear membrane
      - Chromatin
      - Linin
      - Nucleolus
      - Nuclear sap
    - Cytoplasm
      - Plasma membrane
      - Plastids
        - Chloroplasts
        - Leucoplasts
        - Chromoplasts
        - Protein plasts
        - Oil plastids
      - Chondriosomes
      - Vacuole
      - Inclusions
        - Starch
        - Sugar
        - Protein substances
        - Inorganic salts
        - Organic acids
        - Mineral crystals
        - Anthocyanin pigments

The inclusions mentioned above represent inert matter.

Protoplasm.—The term protoplasm as used in this book is applied to all the living substance in the cell; it includes, therefore, nucleus, or nuclei, and cytoplasm, together with specialized parts, as plastids and plastid primordia. Inclusions such as starch, sugars, oils, fats, mineral crystals, and other demonstrably inert bodies do not represent living substance. The following remarks refer chiefly to the cytoplasm.

When seen with the microscope, cytoplasm in live cells appears as a thick, viscid substance of the consistency of glycerine or strained honey

at room temperature. The ground substance, including the plasma membrane lying next to the cell wall, is colorless and homogenous. The plasma membrane and a layer of variable thickness lying next within the membrane are of firmer consistency and always stationary. The inner mass of cytoplasm is more fluid, and grayish granular in appearance, owing to the presence of numerous small, opaque bodies such as plastid primordia and other small granules whose character is not known or not well understood. When cytoplasmic movement is observed, it is this more fluid portion that is in motion. The movement is recognized by the change in position of the visible granules, or by the movement of larger plastids and other bodies located in the parts that are in motion.

In composition, protoplasm is made of water and solid substance. Of the dried substance, one-third to one-half is protein, the remainder being composed of fatty bodies, sugars, and other carbohydrates, organic acids and bases, and salts of potassium, magnesium, calcium, sulphur, phosphorus, etc. The chemical composition of protoplasm is not known. It is admittedly very complex. Any attempt to indicate by a chemical formula a molecule of protoplasm would be useless from our standpoint.

The botanist knows protoplasm chiefly from observations of its visible structure, and from its various physical and physiological manifestations. Protoplasm is capable of absorption, digestion, assimilation, and excretion; it is automatic and sensitive, or irritable; that is, it is capable of responding to stimuli; it has the power of growth and reproduction. By saying that it is automatic, we mean that its source of activity comes from within. Protoplasm grows, not as a crystal by the addition of material to the outside, but from outside materials taken in and there converted into its own substance. It is the only known substance that can reproduce itself, and only living protoplasm can produce other living protoplasm.

Many of the phenomena of living protoplasm, such as the splitting of chromosomes and the dividing of chloroplasts, cannot at present be explained in terms of physics and chemistry. Mechanistic explanations as known at present are insufficient.

Collodial Character.—It was stated in the foregoing that protoplasm is a fluid. In order to gain some knowledge of the kind of fluid represented by protoplasm, certain fundamental facts concerning fluids in general may be useful.

When a lump of sugar is dissolved in water, the particles of sugar become dispersed to the fineness of the molecule. If a lump of salt be thrown into the water, the particles of salt will not only disperse to the fineness of the molecule (NaCl), but dispersal will continue even beyond

this so that some of the molecules are separated into the elements, sodium (Na) and chlorine (Cl). These two elements are then said to be dissociated. The elements of the sugar molecule do not become dissociated in water. In either case we have, however, a *perfect* or *homogenous*, solution. The substance dissolved, in this case salt or sugar, is spoken of as the *solute*, and the medium of dispersal, which in this case is water, is the *solvent*. Substances like sugar, salt, etc., which crystallize on solidifying from a solution, are called *crystalline* substances, and they are said to represent the crystalloid condition. If, on the other hand, glue or gelatin, for example, be dissolved in water, it will be found that these bodies do not dissolve down to the molecule, or, if so, rarely beyond the molecule. The ultimate particles of dispersal are usually larger than the molecule. Such solutions are said to be *imperfect*, or *heterogeneous* solutions.

If perfect solutions, such as those of sugar or salt, be examined with the ultramicroscope, they will appear perfectly clear, while a dilute solution of glue, clear to the naked eye, when thus examined with the ultramicroscope, reveals numerous small particles floating in the fluid, just as particles of dust are seen in the air when a beam of light is admitted to a darkened room.

Such bodies as glue, gelatin, and the like, which do not crystallize on solidifying from solution, are called *colloids*. Certain substances may sometimes exist in the crystalloid and sometimes in the colloidal condition. The conclusion is that colloid and crystalloid represent different conditions of diffusibility. Diffusibility, therefore, is regarded as a *condition* of matter when minutely subdivided, or in solution in some liquid, as contrasted with its state or condition when existing alone. The *state* of a substance may be gaseous, liquid, or solid; its *condition*, when in solution, may be either crystalloid or colloid. When it is said, for example, that enzymes are colloids, the meaning is that enzymes exist in the colloid condition, and not that enzymes represent a definite kind of substance having the group name *colloids*.

Meaning of the Term, Phase.—When the particles of a substance are distributed through the mass of another substance, the mixture represents a *two-phase system*, composed of the *disperse phase*, or substance, and the *continuous phase*, the latter being the medium of dispersal. When the medium of dispersal is a liquid, and the disperse phase a gas, a *foam* results; when the disperse medium is a liquid and the disperse phase a liquid, an *emulsion* results, as when finely divided particles of oil are dispersed in water or other fluid. If the disperse phase be a solid, and the medium a liquid, we have a *suspension*. When the colloid mixture is in the form of a fluid and mobile, it is known as a *sol;* when it is a semi-solid, it is called a *gel*.

If two or more substances are independently dispersed in a common medium, and the behavior of each is independent, there may exist not only a two-phase system, but a poly-phase system.

In a general way, some of the important differences between the crystalloid and the colloid condition may be indicated in the following table:

Crystalloid	Colloid
Crystallizes on solidifying	Does not crystallize on solidifying
Disperses to the molecule or further	Does not disperse to the molecule
Osmoses readily	Does not osmose readily
Boiling point higher than that of the solvent	Boiling point about the same as that of the solvent
Does not form a gel	Forms a gel
In molecular motion	In Brownian movement

In applying these very elementary concepts to the living substance in the cell, it may be said that protoplasm constitutes a polyphase emulsion colloid. It must be borne in mind that the cell sap, which is not living protoplasm, together with dissolved crystalline substances is something different from the firmer framework of protoplasm that remains when cells are killed and dehydrated. The firmer framework of protoplasm is chiefly in the form of gels. The plastids, chromatin, and chromosomes, the nucleolus, the spindle fibers, the plasma membrane, and the denser cytoplasm lying next to it, are gels. The more movable parts doubtless represent a sol, or sols, while lipoid substances may be in the form of emulsions.

Such parts of the protoplasm as plastids, chromosomes, and the nucleolus, which may be seen in the living cell with the aid of the microscope, and whose independent existence and behavior can be traced through their different transformations are more readily conceived as gels, inasmuch as the independent existence of each is observable as a semi-solid, or jelly-like, body. Beyond these elementary conceptions we do not find it profitable to go, for the principles of physics and chemistry do not, at present, suffice for the explanation of many of the manifestations of living protoplasm.

Protoplasm differs from the materials with which the physicist or the chemist works in one profound respect: it is alive, and it is the only substance known that manifests life. Its manifestations of life are perceived objectively through its sensitiveness, or irritability, and through its growth and reproduction. The power of growth and reproduction and response to stimuli all come from within, and not from the environment, although these manifestations may be modified by surrounding energy. In short, protoplasm is automatic, and the thing which makes it

automatic is the fundamental principle of growth and development that we call life. Attempts to explain the manifestations of protoplasm, which do not employ the materials and methods known to science, pass into the realm of purely abstract or subjective speculation.

Movement of Protoplasm.—Having thus learned something of protoplasm as a fluid, we may now turn our attention to certain movements to be readily observed within cell walls, and in naked cells, or in naked masses of protoplasm.

In such cells as those of the leaf of Elodea mentioned in the beginning of this chapter, or in suitable cells of the Eel-Grass, Vallisneria, or the algae, Chara and Nitella, protoplasmic movement within closed cells may be easily recognized by the fact that the chloroplasts, or other large masses of granular matter, are carried along. In cells of Elodea, for example, the character of the movement is indicated by the chloroplasts which are located in the inner layer of cytoplasm. These are seen to pass down one side of the cell, glide around across the end, and return along the other side. Continuous movement in this manner is known as *rotation*. It is evident that there are two lines in the cell, on one side of which the protoplasm moves in one direction, and on the other side in the opposite direction. This is the *neutral line*. The neutral line is very evident in cells of Nitella, in which the chloroplasts are stationary, being located in the dense, immovable layer nearer the plasma membrane. The neutral line appears as a clear strip owing to the absence of chloroplasts. In Nitella, as well as in some other plants, the nucleus is carried along in the moving cytoplasm.

Among higher plants a different kind of protoplasmic movement generally prevails. In the cells of the stamen hairs of the Spiderwort (Tradescantia), or the epidermal hairs of the squash, the cytoplasm is not only arranged in a wall layer, but several strands may traverse the large central vacuole (Fig. 5). Careful observation will reveal the fact that cytoplasmic streaming may be going on in two or more directions in the cell at the same time. Movement which is going in one direction in a given strand may in a short time be reversed. This form of movement has been called *streaming*, or a circulatory movement. In the tubular filaments of certain fungi, such as the common bread mould, the entire mass of moving protoplasm streams first in one direction then, after a rather sudden stop, in the reverse direction. The shifting of the movement back and forth seems to be influenced by the unequal loss of moisture in different parts of the long tubular cells.

Certain lower plants, and the reproductive cells of lower, as well as some of the higher, plants, have the power of locomotion, due to the movements of very slender cytoplasmic threads, known as cilia, which lash

the water in a definite manner. The motion of cilia is styled *ciliary* movement. Another form of protoplasmic movement is observed in such naked cells as in the animal, Amoeba, or in the plasmodium of slime moulds. Here the mass as a whole, or in part, moves by a flowing or creeping movement, the *ameboid* movement.

Protoplasmic movements, though automatic, are influenced, or completely inhibited by factors in the environment. Cold retards, and heat accelerates, movement within certain ranges. Observations carried out by the author on cells of the leaf of Vallisneria showed that from 0 to 13° C. movement was nil or very slow. The rate increased with the rise of temperature to the maximum which was reached at 38°. With further increase in temperature the rate of movement decreased until it ceased at 49°.

If cells in which movement is going on be anaesthetized by means of chloroform, or ether, movement will cease. In general, movement will not occur in cells deprived of oxygen.

Pulsating Movements of Vacuoles.—In localized regions of the cells of lower plants, such as the Algae, movements are to be seen which are produced by certain small vacuoles. Near the anterior end of swarm spores of certain algae one or more minute pulsating vacuoles may be present which appear and disappear rhythmically at short intervals. They empty suddenly, then reappear and slowly increase to their full size. Pulsating vacuoles have been described in detail in the conjugating cells of Spirogyra by Lloyd. Their activity there is regarded as facilitating the union of the gametes.

Nuclear and Cell Division.—We may now direct our attention to some of the processes by which cells and nuclei increase in number. It has long been known that new cells and new nuclei may arise only by the division of pre-existing cells and nuclei. There are two methods of nuclear division, namely, direct nuclear division, or *fragmentation*, and indirect nuclear division, or *mitosis*. Of the several forms of cell division a few of the well-known types will be briefly described in the following paragraphs.

Direct Nuclear Division.—In direct nuclear division the nucleus divides merely by constriction. The resulting nuclei may often be of unequal size. Direct nuclear division occurs only in older cells that have passed into a purely vegetative condition. Such cells have lost the power of growth and division; they do not serve as a starting point for the development of new plants or new organs.

Mitosis, or Indirect Nuclear Division.—The important steps in mitosis may be indicated as follows: in figure 13, A, the chromatin is seen to be distributed upon the linin threadwork in small irregular lumps or granules

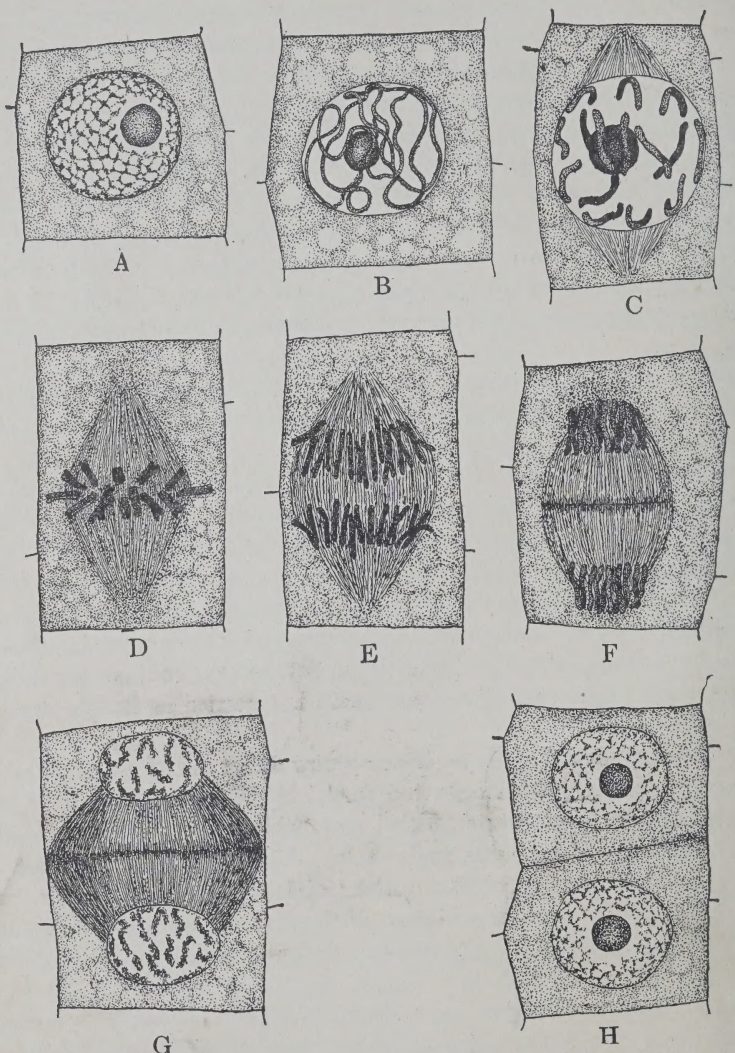


FIG. 13.—Nuclear and cell division in the root tip of the onion (*Allium cepa*). A, nucleus in resting stage. B, the chromatin spirem has been formed. C, the spirem has segmented crosswise into the chromosomes. D, the spindle has been formed and the chromosomes have split lengthwise. E, anaphase: the daughter chromosomes passing to the poles of the spindle. F, telophase: the daughter chromosomes have arrived at the poles, and a cell-plate has been formed. G, daughter nuclei have been formed, and the cell-plate extends across the cell. H, two daughter cells.

of varying size. When the chromatin is in this finely divided state, the nucleus is said to be in the *resting* stage. One or more nucleoli may be present. As the process of division progresses, the chromatin granules come to be so arranged as to form a definite cord, or thread, called the chromatin *spirem* (Fig. 13, B). During this process the quantity of chromatin has increased somewhat. In the cells here under consideration the spirem is a continuous thread without free ends.

The spirem now segments transversely into a definite number of pieces known as *chromosomes* (Fig. 13, C). In young, or embryonic tissue the number of chromosomes is usually constant for the species. We thus see that the spirem is composed of a definite number of chromosomes united end to end, and in such a manner that the limits of the individual chromosomes cannot be determined.

During the transverse segmentation of the spirem into chromosomes, or sometimes a little earlier, there appears in the cytoplasm, on opposite sides of the nucleus, a sheaf-like cap or mass of very fine fibers. These are derived from the cytoplasm, and they will give rise to the future spindle fibers (Fig. 13, C, D). About this time the chromosomes are seen to be split lengthwise, and the halves of each chromosome thus formed are called daughter chromosomes, or daughter segments. The nuclear membrane now disappears, and the masses of fibers extend across through the nuclear cavity and come together in such a way as to make a sheaf, or spindle. The ends of the spindle, which may converge to a point, are the poles; the transverse plane midway between the poles is the equator. During the formation of the bipolar spindle, the chromosomes are brought into the region of the equator, where they are arranged in a plane and sometimes placed radially like the spokes of a wheel (Fig. 13, D). The chromosomes thus arranged in the equator form the nuclear plate. From each daughter segment (daughter chromosome) a small bundle of spindle fibers extends to the pole toward which that segment is soon to pass. Other spindle fibers extend continuously from pole to pole without being attached to any chromosome. In the meantime the nucleolus has disappeared.

The daughter chromosomes now separate and pass to the poles, one of each going to one pole and the other to the opposite pole (Fig. 13, E, F). The two resulting nuclei will consequently have the same number of chromosomes and the same quantity and quality of chromatin material. Such a nuclear division is an *equational* division.

As the daughter chromosomes reach their respective poles, they generally become closely crowded together, and new nuclear membranes are soon formed, thus outlining the two new nuclei (Fig. 13, G). The spindle fibers connecting the two nuclei at this stage are designated as the *connecting* fibers. The chromosomes of each daughter nucleus now fragment

and reticulate, by the formation of vacuole-like spaces within, into smaller, lump-like, irregular pieces, which are generally connected by slender strands to form a net or *reticulum*. The very fine colorless threads connecting the larger chromatin masses or granules are linin. The breaking up into smaller pieces continues until the chromatin is resolved into finely divided granules held upon the linin threadwork like that of the resting nucleus. In the meantime a nucleolus has appeared in each new nucleus. These new nuclei are the *daughter nuclei* (Fig. 13, G, H).

We may now turn our attention to the nucleolus which was present in the parent cell (Fig. 13, A). During the process of division just described, at or before the spindle stage, the nucleolus disappears as such. A new nucleolus, or nucleoli, reappears in each daughter nucleus, usually closely associated with the chromatin (Fig. 13, H). The author is convinced that the nucleolus represents reserve material which may be used by the nucleus as needed, and especially in connection with the development of the chromatin. In well nourished cells there seems to be more nucleolar material than in cells poorly nourished. In well nourished spore-bearing cells of certain higher plants (Lilium) when one or more large nucleoli are present in the nucleus, many small nucleoli are observed scattered throughout the cytoplasm during mitosis. This seems to indicate that the nucleoli are either dissolved or broken up into smaller parts.

Types of Cell Division.—Of the various types of cell division, and their modifications, the following will be described: division by cell plates, constriction, cleavage furrows, and internal cell division.

Division by Cell Plates.—Division of cells by means of cell plates is the commonest and most widely occurring form among plants. An excellent illustration is to be found in young tissues, such as the growing end of roots, and we shall select the root of the onion, as in the case of nuclear division.

When, as seen in Fig. 13, F, the daughter chromosomes have reached the poles of the spindle, and during the formation of the daughter nuclei, a transverse line appears in the equatorial region of the connecting fibers (Fig. 13, G).

This line, which is the edge of a disk, is the *cell plate*. It begins as a small, circular disk at the center of the system of connecting fibers, and progresses in all directions until it meets the plasma membrane of the cell. The cell plate is of the nature of a plasma membrane. It splits, forming two plasma membranes, between which the cell wall is laid down (Fig. 13, H). In this type of cell division, therefore, the cell-plate is formed by the connecting fibers.

Division by Constriction.—Division by constriction is found in certain algae, as in the common Cladophora. It occurs also in groups of plants

widely separated in relationship. In this form of division cell plates are not present. In fact, nuclear and cell division occur at different times. The process is made clear in Fig. 14, A-C. At a point usually midway between the ends of the cell, the cytoplasm is seen to be pushed away from the lateral wall of the cell as if constricted. At this constriction a new transverse wall is being built up by the cytoplasm in the form of a ring. The constriction becomes deeper, and the new wall broader, progressing toward the center (Fig. 14, B). The new transverse wall is now a circular disk with a circular opening in the center. Finally the disk is

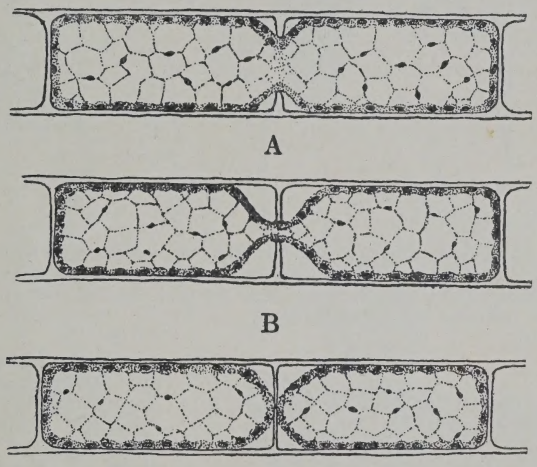


FIG. 14.—Cell division by constriction in Cladophora. A, transverse constriction of cytoplasm near middle of cell, and beginning of transverse ring of new wall. B, further progress in division. C, division complete.

completely closed, and the new wall is complete (Fig. 14, C). The wall layer of cytoplasm soon moves out into the corners of the respective cells.

This mode of cell division occurs in a slightly modified form in Spirogyra. In this plant, however, the division of the cell follows the division of the nucleus, since the cells are uninucleate.

Division by Cleavage Furrows.—Division by cleavage is accomplished by means of surface furrows that begin at the plasma membrane and at the vacuoles. They meet and divide the common cytoplasm into portions containing one or more nuclei. An illustration is found in the large cell which bears spores in certain common moulds. This is a multinucleated cell (Fig. 15, A). Proceeding from the periphery of the cell and from vacuoles, the furrows divide the cytoplasm into numerous cells (Fig. 15, B). Certain details of the process are shown in Fig. 16. In Fig. 16, A, which is a portion of the initial cell, surface cleavage furrows

extend into the cytoplasm, meeting vacuoles in such a manner that the entire cytoplasm of the large cell is divided into large irregular portions

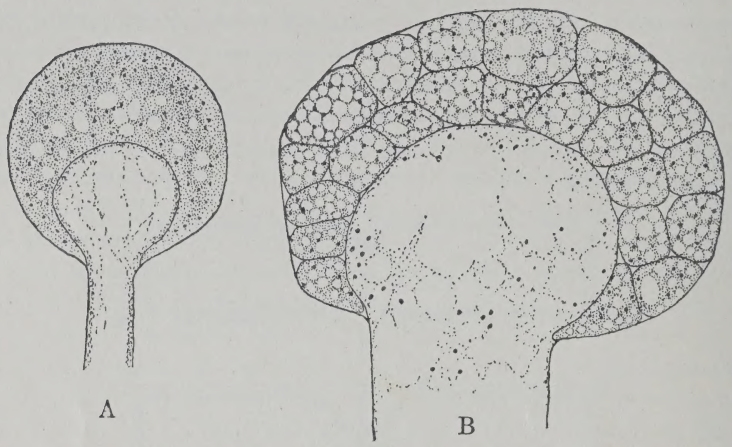


FIG. 15.—Cell division by cleavage furrows. A, young sporangium of common mould, consisting of a large multinucleated cell, the dots representing the numerous nuclei. B, sporangium of mould (*Sporodinia grandis*) divided into rounded cells by surface cleavage furrows. (B, after Harper.)

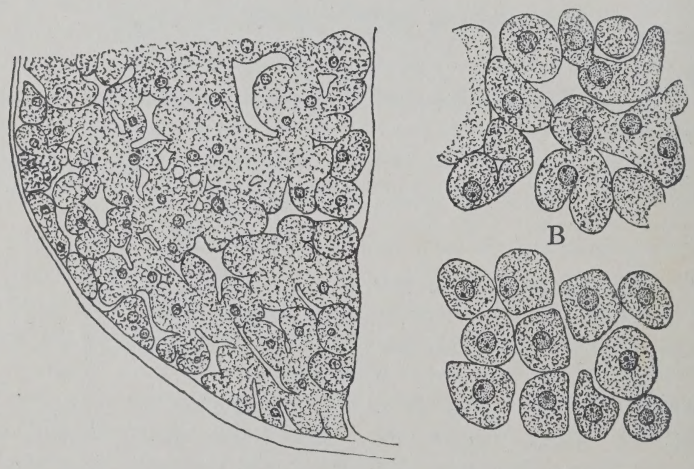


FIG. 16.—Cell division by cleavage furrows. A, portion of a developing sporangium of a mould (*Pilobolus crystallinus*) showing how surface furrows meet those from vacuoles, cutting the mother cytoplasm into large, irregular masses. B, further cleavage of these masses. C, cells resulting from the progressive cleavage. (After Harper.)

containing from one to several nuclei. In these masses cleavage continues until the large initial cell is divided into the ultimate cells (Fig. 16, B, C).

Free Cell Formation.—Free cell formation consists in the cutting out, or delimitation, of cells from the common cytoplasm of the given cell by the activity of spindle fibers that persist in connection with the nuclei. As an illustration we shall select the initial cell of the spore sac (ascus) of a common cup fungus.

Here, as seen in Fig. 17, the spindle fibers, or polar radiations, attached to the nuclei curve around outward and backward to form plasma membranes, thus cutting out cells from the mother cytoplasm.

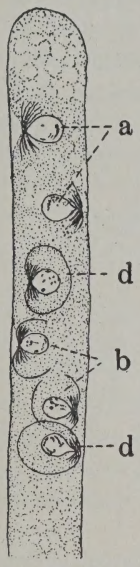


FIG. 17.—Internal cell division. Portion of a young spore sac (ascus) of the cup fungus, *Lachnea scutellata*, in which the cells are delimited from the mother cytoplasm by the action of the persisting spindle fibers attached to the nuclei. *a*, nuclei with attached polar radiations; *b*, cell partly delimited; *d*, *d*, cells completely formed. (From Harper.)

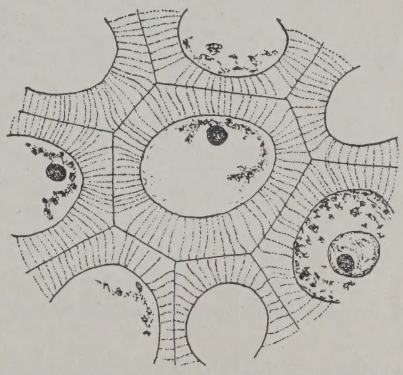


FIG. 18.—Cells of endosperm of persimmon (*Diospyros discolor*) showing numerous fine cytoplasmic threads (plasmodesmi) extending through the cell wall from cell to cell.

The Cell Wall.—When the structure of the firmer parts of the higher plants is taken into consideration, the most outstanding feature is the cell wall. In only a very small part of a tree or woody bush do the cells possess living protoplasm, the bulk of the plant being composed of the walls of cells from which the living substance has almost wholly or quite disappeared. In cells of all plants, the cell wall, if present, is dead material, which was, of course, built up by the living substance; it is the house in which the living occupant dwells.

In both high and low forms the walls between neighboring cells in certain individuals, or in certain parts of those individuals, are perforated by small holes, *pits*, through which delicate threads of cytoplasm (*plasmodesmi*) extend from one cell to another (Fig. 18). In this manner the cells of certain tissues are in direct cytoplasmic communication with each other. In some plants, such as red sea-weeds, the cytoplasmic connections between cells are large and easily demonstrated. It should be remembered, however, that all living cells of plants are not connected by living substance, and the whole plant cannot be regarded as a continuous plasmodium.

The primary walls of cells are usually thin and delicate. As the cells mature in many tissues, the walls become very thick, owing to the formation of secondary thickening layers (Fig. 19). The secondary thickening

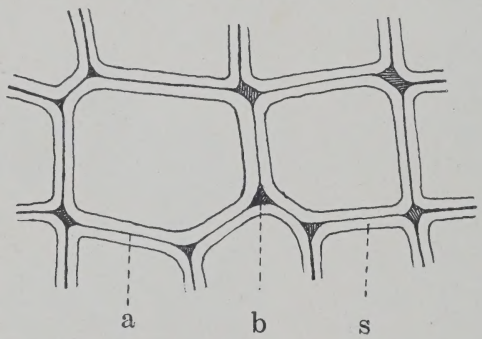


FIG. 19.—Cells of pine wood, showing middle lamella, *a*, *b*, and secondary thickening layer of cell wall, *s*.

is accomplished by the deposition of successive layers of cell wall substance, or by the intercalation of new particles of cell wall substance between those already present.

The Middle Lamella.—The middle plate in walls of neighboring cells of mature tissue is of a different composition from that of the secondary thickening, and this middle plate is the *middle lamella*. This fact is clearly shown in Fig. 19, *a*. When intercellular spaces are not present, the middle lamella is much thickened at the angles of the cells, as shown by the gusset-like thickening at *b*. The middle lamella occupies the position of the primary wall of young cells, but it is not the primary wall alone. The primary wall has undergone changes due to the infiltration and addition of various other substances. The middle lamella is soluble in reagents that do not readily dissolve the secondary thickening of the walls, *s*. For example, a mixture of chlorate of potash and nitric acid will dissolve the middle lamella, while the secondary thickening is more resistant. On the contrary, sulphuric acid readily dissolves the secondary thickening,

but not the middle lamella. The maceration of tissues is accomplished, therefore, by the softening, or dissolution, of the middle lamella. The retting of flax in the field is brought about by the dissolution of the middle lamella as a result of decay or oxidation.

The varied character of cell walls is not due wholly to differences in thickness or configuration, but to their chemical composition as well.

Cellulose.—The fundamental substance in cell walls is cellulose,* which chemically is a carbohydrate with the formula $(C_6H_{10}O_5)_n$. The walls of the pith of the elder, the pith of the sunflower, and the fiber of the cotton plant are examples of a rather pure cellulose. It is to be understood that cellulose exists in various forms. In seeds of the date and other palms a form of cellulose, *hemicellulose*, constitutes the reserve food. This is easily digested when the seed germinates, but in the dried form it is hard and stony, sometimes being spoken of as "vegetable ivory." Cellulose turns blue upon the application of chlor-zinc iodine or iodine and sulphuric acid.

Pectose, Pectine.—Cell walls are rarely composed of pure cellulose. The middle lamella, for example, contains in addition to cellulose pectic substances such as pectine and pectose. Pectic substances are abundant in the tender cell walls of such fruits as quinces, apples, pears, currants and gooseberries, and in fleshy roots of such vegetables as carrots and parsnips. Pectine and other pectic substances are soluble in water, and when dissolved in concentrated solutions they set into jellies on cooling. Characteristic stains for cell walls containing pectine and pectose are ruthenium red and haematoxylin, the former giving a rose and the latter a blue color.

Cell walls may contain other substances in addition to cellulose such as lignin, cutin, and suberin. These will be referred to later in connection with tissues whose walls they characterize.

TOPICS FOR REVIEW AND DISCUSSION

Why is Elodea called an aquatic plant?

Why is it suitable for the observation of living cells?

How many sides has a cell of the leaf of Elodea? Are these cells flat, like a sheet of paper?

What are chloroplasts?

What is the color of pure cytoplasm?

How much of the cell volume of leaf cells of Elodea is vacuole?

Where is the bulk of the cytoplasm located in the cells of the leaf of Elodea? What part of the cytoplasm moves?

Do the chloroplasts move as a fish swims? Explain.

* Cell walls of fungi are composed of a modified cellulose, which in some respects bears a resemblance to animal chitin.

Who was one of the first persons to discover that plants were made of cells? What tissue did he use in his study? Was this person a botanist? When did he live?

Who was said to have discovered the living substance in the cell?

Who gave it the name *protoplasm?* Is the term cell an appropriate name?

How many and what plastids occur in cells?

What is the plasma membrane as used in this book?

What different structures make up the nucleus?

What are plastid primordia?

How do adult chloroplasts multiply?

In what is chlorophyll readily soluble?

Name three pigments in chlorophyll. What is a pigment?

What is the difference between chloroplasts and leucoplasts? Can one change into the other?

What is an etiolated plant?

Why will grass turn white under a board laid upon the lawn?

The book states that some plants are brown, some red and some blue. To what is each of these colors due? Where are these pigments located in the cell?

What are cell inclusions? Do they represent living or inert bodies?

Name some of the physical properties of protoplasm. Some physiological properties.

What is meant by the term solvent? Solute?

What is a perfect or homogeneous solution? An imperfect or heterogeneous solution? Distinguish between colloid and crystalloid.

What is a *sol?* A *gel?*

Protoplasmic movements are referred to as rotary, streaming, ciliary, and amoeboid. Distinguish each from the others. Which pertain to movements within cell walls, and which outside of the cell wall? What is the neutral line?

What physical conditions of the environment affect plasmic movements?

Distinguish between ordinary vacuoles and pulsating vacuoles.

Do all cells have the same number of nuclei?

How do nuclei increase in number?

What is the chromatin spirem?

What are chromosomes?

Is there anything definite in regard to their number in the nuclei of a given species?

When a nucleus divides how does it happen that the two resulting nuclei may have the same number of chromosomes?

What is meant by the expression "daughter nuclei"?

What is the nuclear plate? The cell plate? Connecting fibers?

How many methods of cell division are described in the text? How does each method differ from the others?

What makes up the larger part of a bush or tree, the cell walls or the protoplasm?

What is the middle lamella?

What are plasmodesmi?

What is the fundamental substance in cell walls? How could you demonstrate its presence?

What is meant by the retting of flax? By the mascerating of wood in making paper pulp?

What is "vegetable ivory"?

CHAPTER III

THE LEAF

We learned in the first chapter that the three great members of a typical seed-bearing plant are the leaf, the stem, and the root. We saw also that the leaf was an expanded lateral outgrowth of the stem, having a bud in its axil. Of the various kinds of leaves the foliage leaf is by far the most numerous and important.

The Foliage Leaf.—A foliage leaf may possess the following parts, the blade or *lamina*, the leaf stalk or *petiole*, and in many cases, *stipules*, which are outgrowths from the base of the petiole (Fig. 20, A). The stipules are sometimes very large, larger even than the blade or blades, as in the garden pea, (Fig. 21, B, *s*), and, on the other hand, stipules may be absent. When the blade is attached directly to the stem, the petiole is absent, and the leaf is *sessile*. A leaf with a single blade is a *simple* leaf, but if two or more blades be present, as in the clover, rose, or common locust, the leaf is compound and each division is a *leaflet*. When the leaflets are arranged in two opposite rows upon the common axis, the leaf is *pinnately* compound (Fig. 21, A, B). A *palmately* compound leaf is one in which the leaflets radiate from the end of the petiole, as in the buckeye, Virginia creeper, and clover (Fig. 21, C).

Venation.—The blade of the leaf is seen to consist of a green substance through which are usually distributed numerous veins. There are two types of veining, net-veined and parallel-veined. In a parallel-veined leaf the veins run from the base of the blade to the apex (Fig. 20, D). In many leaves a single prominent vein extends up through the middle. This vein is called the midrib. From the midrib all the smaller veins arise as branches. The branches may continue to branch and re-branch until a very fine and elaborate network results, which is conspicuously revealed in skeletonized leaves (Fig. 22). When the branches arise right and left from the midrib the leaf is *pinnately* veined. In certain leaves, as in the Geranium (Fig. 20, B), a number of prominent veins extend radially from the end of the petiole out into the blade. Such a leaf is *palmately* veined.

In some parallel-veined leaves like those of Canna and of the banana there is a large central rib from which the smaller parallel veins run to the margin (Fig. 20, E). Between the type of leaf with veins wholly of basal

origin, and that with veins springing from the midrib there are all gradations. There are various gradations also in respect to the curving in these two types. When the veins curve in their course, as in the plantain lily (Funkia) and in Canna, we have *curvinerved* veins. In some parallel-

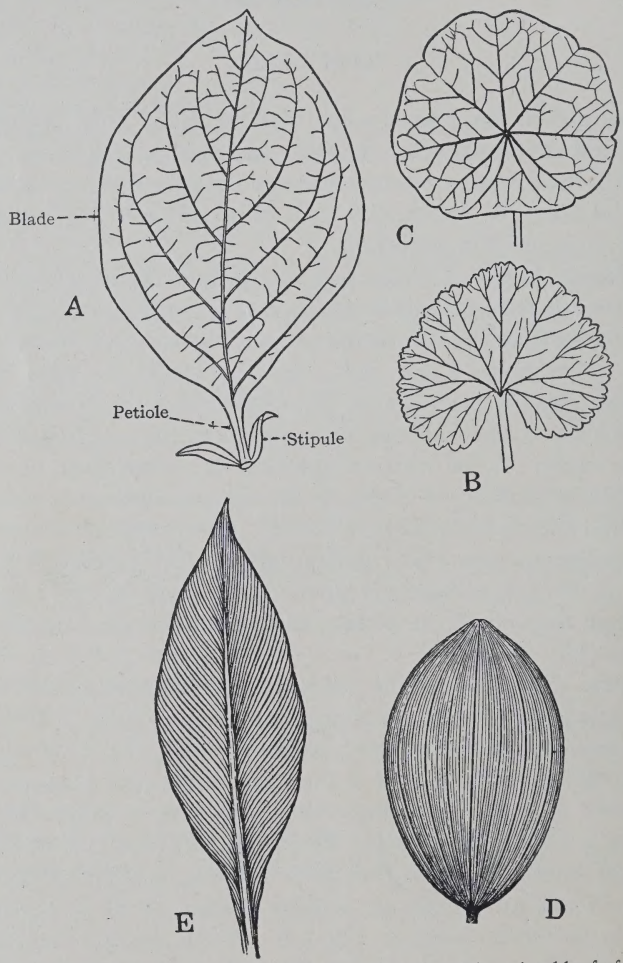


FIG. 20.—Foliage leaves. A, leaf of quince. B, palmately veined leaf of Geranium. C, of Nasturtium. D, parallel veined leaf of Solomon's Seal (*Polygonatum multiflorum*). E, leaf of Canna. (B, C, D, Strasburger, Macmillan Co.)

veined leaves there are fine reticulations between the larger parallel veins. In the Smilax and Dioscorea only the strongest veins are curved, the spaces between being filled with a network of smaller veins. Such leaves form a transition from parallel to netted-veined leaves.

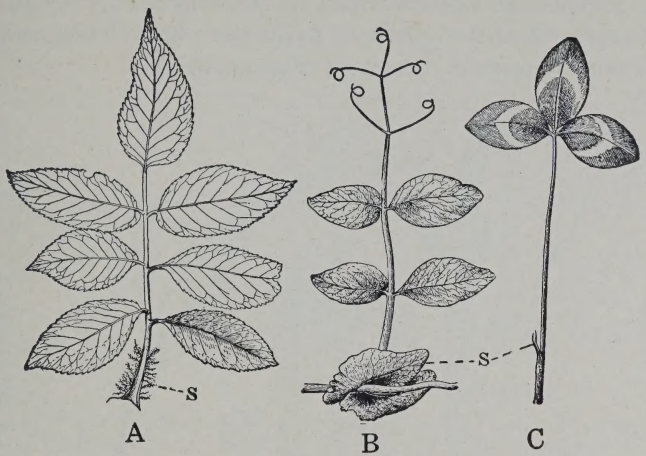


FIG. 21.—Forms of compound leaves. A, odd pinnate leaf of rose. B, leaf of pea; note the large stipules, *s*. C, leaf of clover, with small stipules.

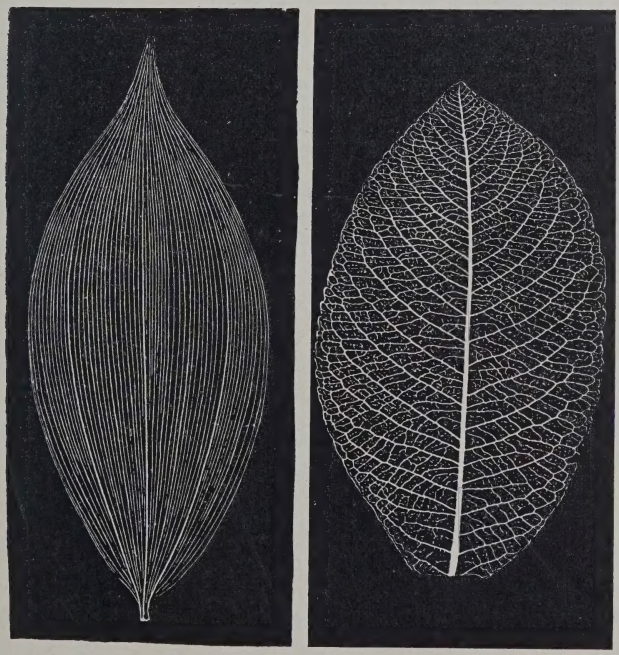


FIG. 22.—Skeletonized leaves. A, parallel venation of Solomon's Seal (*Polygonatum latifolium*). B, pinnately, netted venation of leaf of willow. (After Ettingshausen.)

In the leaves of grasses the petiole of the leaf clasps or surrounds the stem; it is then called the sheath.* At the juncture of blade and sheath there is a small outgrowth, the ligule (Fig. 23, B).

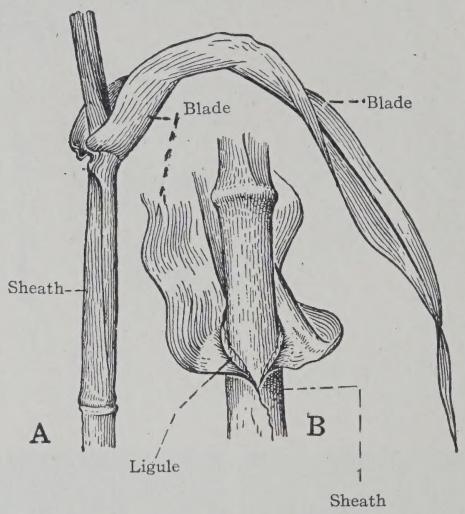


FIG. 23.—Portion of a corn stalk. A, with complete leaf. B, juncture of sheath and blade, showing ligule. (After Atkinson.)

The foliage leaves of pines, spruces, hemlocks, and cedars are needle or awl-shaped. Here the venation is parallel.

Forms of the Leaf Blade.—The leaf blade owes its form largely to the manner in which the base and apex develop, and to the depth and character of the indentations of the margin.

FIG. 24.—Forms of leaves as to outline. A, linear; B, lanceolate; C, oblong; D, elliptical; E, ovate; F, cordate or heart-shaped.

The forms, as to general outline, are shown in Figs. 24 and 25. As to the base of the blade, the chief forms are *halberd-shaped*, *auriculate* and *sagittate* (Fig. 26, A, B, C). The various forms of apex are shown in Fig.

* The sheath is regarded by some authors as a modified leaf base rather than a petiole.

27. The margin of the blade may be *serrate*, *dentate*, *crenate*, *repand* or *undulate*, *sinuate*, and *incised* or *cut* (Fig. 28). Depending upon the depth

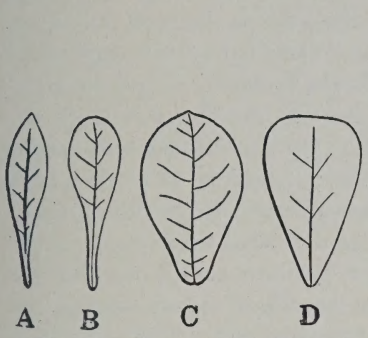


FIG. 25.—Forms of leaves as to outline. A, oblanceolate; B, spatulate; C, obovate; D, cuneate (wedge-shaped).

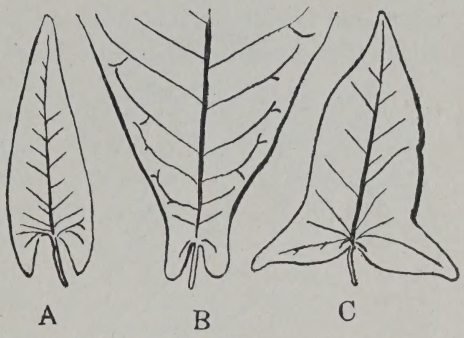


FIG. 26.—Forms of bases of leaf blades. A, halberb-shaped; B, auriculate; C, sagittate.

to which the indentations extend towards the midrib, leaves are *lobed*, *cleft*, *parted*, and *divided* (Fig. 29).

Connate and Perfoliate Leaves.—In some plants like that of the bellwort, Uvularia, the leaf develops in such a manner that the edges of the

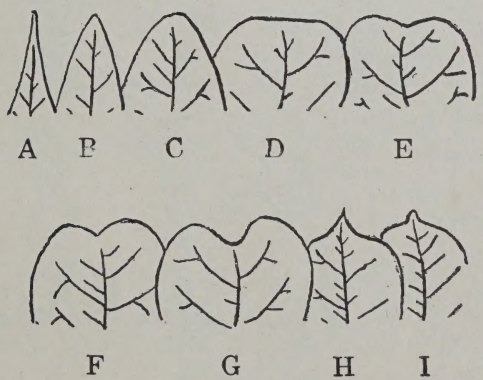


FIG. 27.—Forms of the apex of leaves. A, acuminate; B, acute; C, obtuse; D, truncate; E, retuse; F, emarginate, notched; G, obcordate; H, awn-pointed or bristle-pointed; I, cuspidate.

base are so grown together that the stem seems to run through the blade of the leaf near the basal end (Fig. 30, A). In the case of the wild honeysuckle we have a pair of opposite leaves with their broad bases grown together. The appearance is that of a large rounded leaf with the stem running through the center. Such leaves are said to be *connate-perfoliate*.

The fact that two leaves are involved is readily understood by comparing the lower and upper leaves on the same stem (Fig. 30, B).

Equitant Leaves.—While the leaves of most broad-leaved plants spread horizontally, with one face to the sky and the other to the earth, there are others that present their tips to the sky and their flat surfaces right and left to the horizon. These are equitant leaves, and the Iris is an example. On careful inspection near the base, it will be seen that each leaf has grown folded together lengthwise, so that what would be the upper surface is within, except near the base where each leaf stands astride the next younger one. This straddling over each other, like a man on horseback, as seen in cross section of a bud, led Linnaeus in his fancy to call these *equitant leaves*.

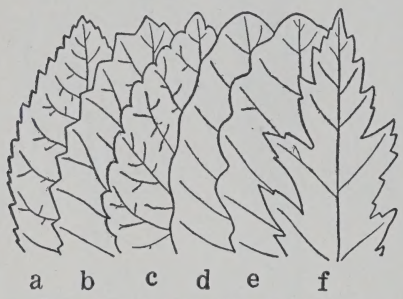


FIG. 28.—Forms of leaf margins. *a*, serrate; *b*, dentate; *c*, crenate; *d*, repand or undulate; *e*, sinuate; *f*, incised or cut.

Arrangement upon the Stem.—When but one leaf develops from each node of the stem, the leaves are said to be *alternate*. A line passing around

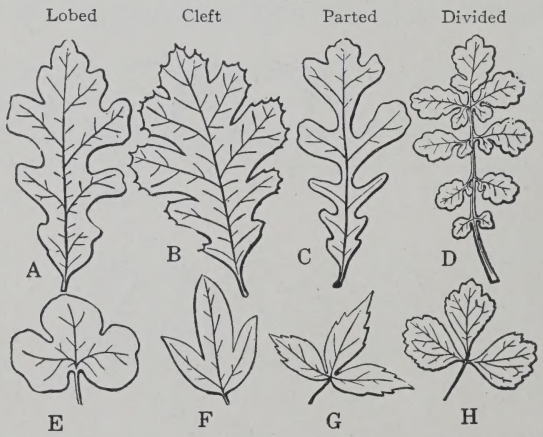


FIG. 29.—Forms of leaf margins. A, lobed; B, pinnately cleft; C, pinnately parted; D, pinnately divided; E, palmately lobed; F, palmately cleft; G, palmately parted; H, palmately divided.

the stem through the base of each leaf will make a spiral, and the leaves are *spirally* arranged (Fig. 31, A). In some plants two leaves appear at the node; they are then *opposite*. Leaves are *whorled* when three or more spring from a node. Opposite and whorled leaves are *cyclic* in arrangement (Fig. 31, B, C).

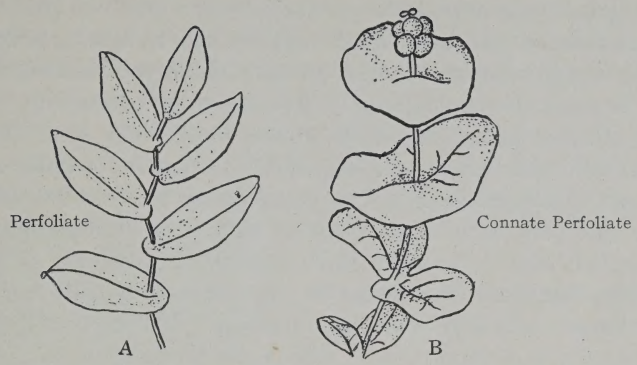


FIG. 30.—Connate and Perfoliate Leaves. A, shoot of Uvularia with perfoliate leaves; B, shoot of wild honey suckle with connate-perfoliate leaves.

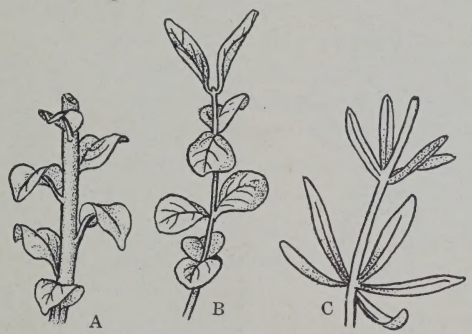


FIG. 31.—Arrangement of leaves upon the stem. A, alternate (spiral); B, opposite (cyclic); C, whorled (cyclic).

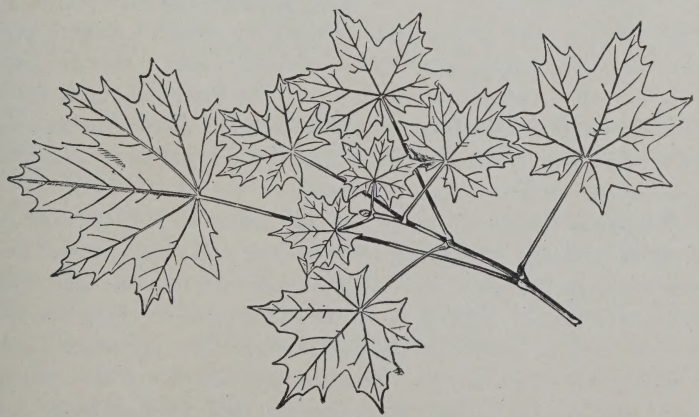


FIG. 32.—A spray of hard maple, showing adjustment of the leaves as to size of blades and length of petioles. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

Light Arrangement.—Leaves are usually oriented upon the stem in such a manner that they may shade each other as little as possible. Those of the Virginia creeper, spread out upon the surface of a building, wall, or tree trunk, are so arranged as to form a sort of leaf-mosaic. The same is true also of the small leaflets of the Maidenhair fern. In our forest trees, the leaves borne by horizontal branches are of different sizes with petioles of different lengths, and the large and small leaves are so adjusted as to interfere as little as possible with their illumination. A striking example is seen in the hard maple as shown in Fig. 32.

The Horizontal Position.—In the majority of plants, as stated, the position of the foliage leaves is horizontal. The upper side consequently receives the direct rays of the sun, or it is more strongly illuminated than the lower side. As long as the leaf is capable of growth, it may change its position so that the proper surface faces the impinging light rays. A plant growing near a window will be found with its leaves facing the light; but if it be turned around so as to bring the opposite side to the light, the leaves will soon become adjusted to the new light position. For the same reason the rosette of leaves at the end of the stem of a vigorously growing sunflower plant tends to "follow the sun."

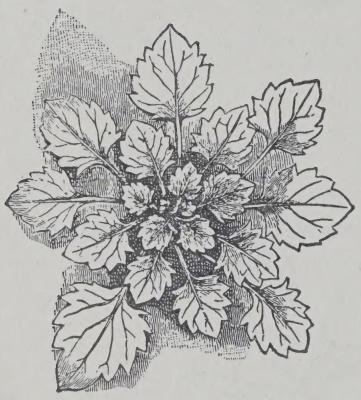


FIG. 33.—Rosette arrangement of leaves in a bellflower (Campanula). (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

The Rosette Habit.—Plants with very short stems, such as are seen in the first season's growth of many biennials, may bear numerous leaves crowded into a rosette, many of which lie flat upon the ground (Fig. 33). The blades of the lower leaves would be completely shaded by those above were it not for the fact that the petioles of the lower leaves are longer than those of the leaves next above, and so on in succession to the uppermost.

The Compass Plants.—Plants like the rosin-weeds (Silphium) of the prairie region and the common prickly lettuce (*Lactuca scariola*) growing in waste places in the open, have their leaves directed vertically upwards with the edges turned toward the intense light, while their flat surfaces face the less intense light of early morning and late afternoon (Fig. 34). Many of the leaves stand with the edges pointing north and south, and because of this fact such plants have received their popular name, *compass plants*.

Day and Night Position.—Most leaves of plants when fully grown are in a fixed position, and they are unable to change it. On the other hand, the leaves of many plants change their position regularly with daylight and darkness, and sometimes between the hours of very intense and less intense illumination. Familiar examples are to be found in the clover, Oxalis, bean, locust, Acacia, and Sensitive Plants. Here the leaflets of the compound leaves droop or fold up together in darkness and spread widely apart in light (Fig. 35). These movements are sometimes referred to as "sleep movements." In many plants the response to the light stimulus is plain, and the functional advantage evident, but in many cases it is not evident. The night position in some cases, at least, affords protection against too rapid cooling owing to rapid evaporation.

FIG. 34.—A compass plant, the prickly or wild lettuce (*Lactuca scariola*). A, the plant is viewed from the south. B, viewed from the east. (After Atkinson.)

Origin and Growth of Leaves. Leaves arise as flat outgrowths from the growing point of the stem (Fig. 36). These small beginnings (leaf primordia) gradually enlarge and take on the shape of the mature leaf. The younger leaves are always overlapped by the older (Fig. 37). In the axils of the young leaves may be seen the beginning of axillary buds. The growing end of the stem with its overlapping leaves of different stages constitutes a bud.

FIG. 35.—Leaf of clover. A, day, and B, night position. (From Darwin, Power and Movement in Plants. Courtesy of D. Appleton & Co.)

As the bud opens, the leaves expand and increase rapidly in size, a phenomenon so noticeable in such trees as hickory, buckeye, horse-chestnut, etc. Generally, the leaf blade enlarges equally throughout its whole extent. In many leaves, however, the tip end matures early, while growth continues for a time in the basal part. The leaves of ferns, however, grow at the tip and so continue to grow until they are mature.

Minute Anatomy of the Leaf Blade.—The typical foliage leaf consists of three great systems of tissue, the *epidermal*, the *ground* tissue, or the *mesophyll*, and the *vascular* tissue, the veins.

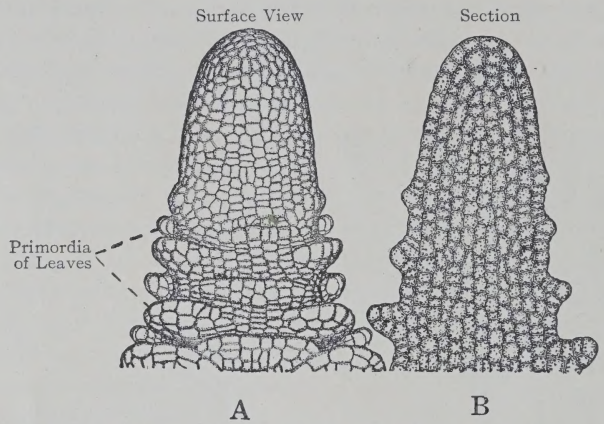


FIG. 36.—The growing end of the stem of the aquatic plant, *Elodea canadensis*, showing the origin of leaves. The larger over-lapping leaves are omitted. A, surface view; B, in section. (Courtesy of Standard Scientific Corp., formerly Scientific Equipment Dept. of Kny-Scheerer Corp.)

The Epidermis.—The epidermis covers the entire surface of the leaf including the edge and the petiole. It may be readily stripped off and examined from the surface with the microscope. Thus observed the epidermal cells of the under side are irregular in shape, with curved or wavy interlocking sides (Fig. 38, A). Conspicuous structures suggesting button holes are numerous. Each of these consists of a narrow slit-like opening, or *pore*, formed by two kidney-shaped cells with their concave edges adjacent. The pore is the *stoma* and the two cells forming it are the *guard cells*. The *stomata* form direct communications between the intercellular spaces within the leaf, which are filled with air, and the external atmosphere (Fig. 39). The guard cells may contain numerous, conspicuous chloroplasts.

FIG. 37.—Longitudinal section of the terminal bud of a young corn plant, the older leaves being omitted. The beginning of an axillary bud is present at the right.

The guard cells are able to open and close the stoma. In so doing they tend to regulate the interchange of gases, and the evaporation of moisture from the inner surface of the leaf. When the guard cells are turgid, more

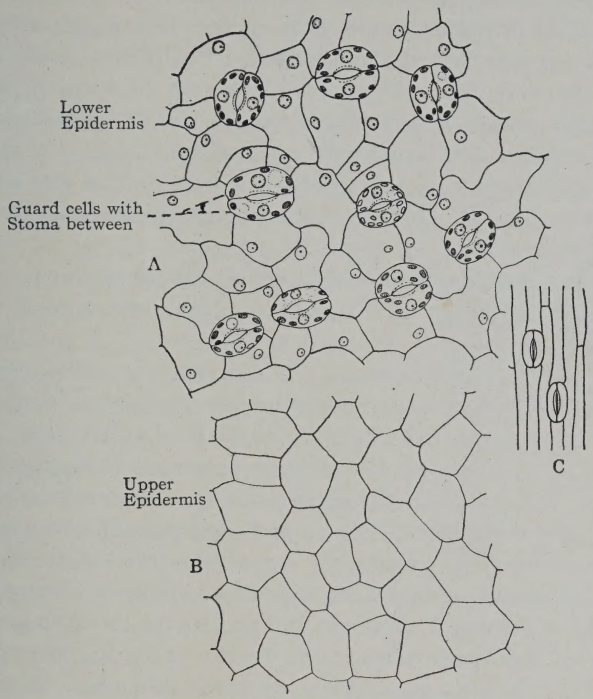


FIG. 38.—Surface view of epidermal cells of Lilac leaf. A, under surface; the guard cells are curved away from each other and the stomata are open. B, upper surface. C, epidermal cells of Lilium showing stomata closed.

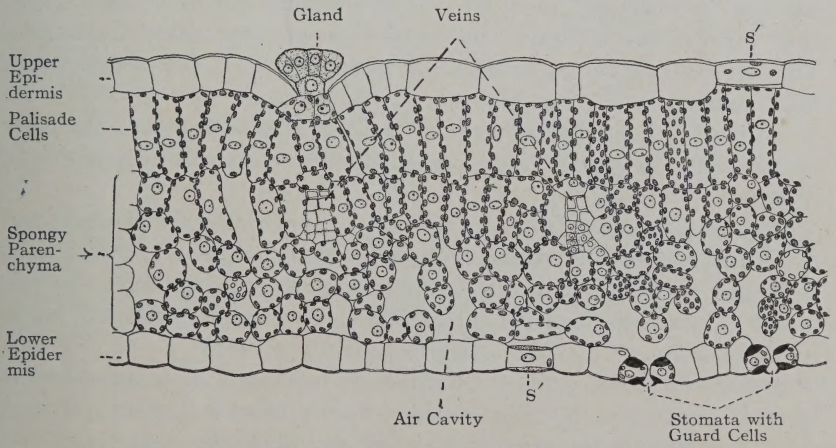


FIG. 39.—Vertical section of the blade of young foliage leaf of Lilac. *s'*, stoma.

turgid than the neighboring cells, the stomata are opened. If the turgor is equal to that of the neighboring cells, or if, by loss of water, all the living cells of the leaf are less turgid, the stomata are closed. Guard cells distended by water curve outwardly thereby widening the opening; when they lose water they tend to become more straight, and the pore is closed (Fig. 38, C). An increase of sugar in the guard cells tends to increase their turgidity, and since sugar accumulates in the cells as a result of photosynthesis, illumination, which increases photosythesis, tends to lead to the opening of the stomata.

The epidermal cells of the upper surface of the leaf are similar to those on the lower side, but they are more regular in outline, and stomata may be entirely absent.

Stomata are usually very numerous. In different plants the number varies from 4,000 to 30,000, sometimes reaching as many as 60,000 to 70,000 in a square centimeter of leaf surface, as in the olive and rape. On the upper side of the leaf they may be wanting or but few in number save in certain groups of plants. In the grasses, for example, there are also many stomata upon the upper side. Stomata are present, although in smaller numbers, on the upper side (that next to the stem) of the sheath of grass leaves. There are, as a rule, no stomata on submerged leaves nor on the underside of floating leaves. In floating leaves the stomata are confined chiefly to the upper surface and to the under surface of the up-turned margins. In some plants they are found in clusters, in others they are uniformly distributed.

In a vertical section the epidermis is seen as a row of cells somewhat uniform in shape and size (Fig. 39). The stomata appear as narrow passages between the outer air and intercellular spaces beneath. The outer layer of the cell walls consists of water-proofing material, the *cutin*. The radial walls also may be thickened in certain plants, and contain cutin. Such walls are said to be cutinized.

In plants of the desert, such as Cacti, Agavas, and others, the layer of cutin may be very thick and cutinization may extend to more deeply lying cells.

Cutin.—The outer layer of the walls of epidermal cells of stems and many fruits, with the exception of very young tissues and root hairs, is composed of cutin. As stated, cutin is water-proofing material. Its role is not so much to keep the surface dry as to prevent the loss of water by evaporation. Chlorzinc iodine turns cutin yellow.

On the surface of fruits and of other parts of various plants, as on the stem of sugar-cane, there is formed a wax or waxy substance. On the surface of such fruits as grapes, apples, and plums the wax constitutes the "bloom" of the fruit. In the case of the sugar-cane wax is especially

well developed at the joints, and appears as fine threads or rods standing at right angles to the surface of the epidermis (Fig. 40).

Wax is dissolved by such solvents as chloroform, ether, benzene, or hot alcohol.

Epidermal Hairs.—From the epidermis of the plant there may develop many hair-like outgrowths (trichomes) of the most varied form and structure. They vary from the simple papillae of the petals of the pansy to large, branched or massive multicellular structures. Many are glandular, producing sticky substances as in the Petunia and tobacco, and in many other plants. The odors of the leaves of some plants are due to secretions from glandular hairs.

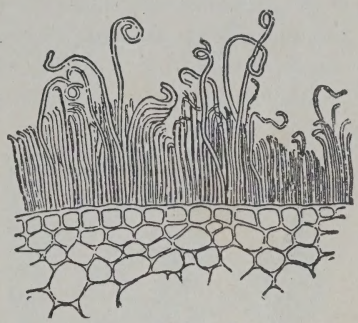


FIG. 40.—Portion of cross section of node of sugar cane showing rods of wax secreted by the epidermis. (From De Bary.)

Fig. 41, C, illustrates glandular hairs of a primrose in several stages of development. The gland of the hop, a saucer shaped scale-like structure, is shown in Fig. 41, A, B. The straw-colored secretion accumulates beneath the

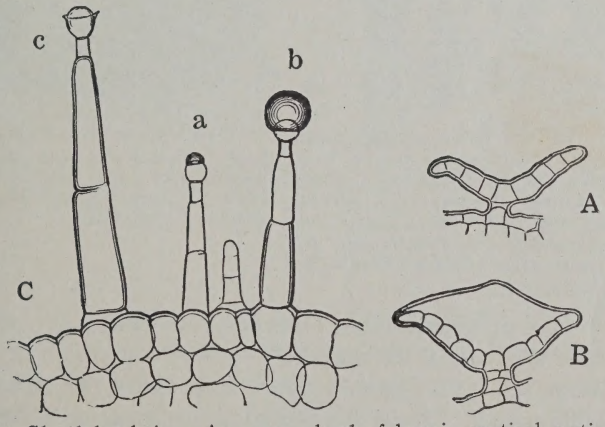


FIG. 41.—Glandular hairs. A, young gland of hop in vertical section; B, older stage of same in vertical section. The secretion (not shown in the drawing) from the cells accumulates beneath the cuticle, pushing it out. C, glandular hairs from petiole of the primrose (*Primula sinensis*) in several stages of development; *a*, beginning of the secretion in the terminal cell; *b*, hair with large quantity of secreted matter; *c*, an old hair after removal of secreted matter. (After De Bary.)

cuticle, pushing it upwards. These glands produce the bitter element of hops known as *lupulin*.

A variety of very interesting epidermal hairs is to be found upon the pumpkin, squash, melon and cucumber vines (Fig. 42, A). A clinging

hair and a stinging hair are shown in Fig. 42, B, C. The white or silvery appearance of the underside of oleaster leaves (Elaeagnus, Shepherdia) is due to the scale like hairs shown in Fig. 43. The glands on the bud scales of the horse chestnut tree produce a sticky substance composed of a mixture of gum and resin.* The woolly appearance of the leaves of the

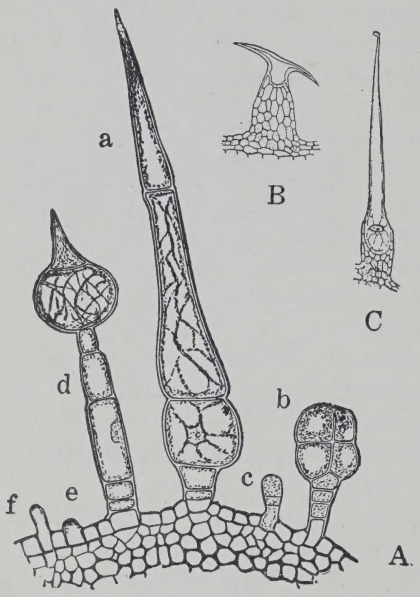


FIG. 42.—Various forms of epidermal hairs. A, from the pumpkin vine; *a*, hair consisting of a row of cells; *b* and *d*, glandular hairs of different ages; *e*, *f*, *c*, hairs in young stages of development; B, climbing hair (*Loasa hispida*). C, stinging hair of nettle (*Urtica urens*). (A, after Prantl, B, C, after Haberlandt.)

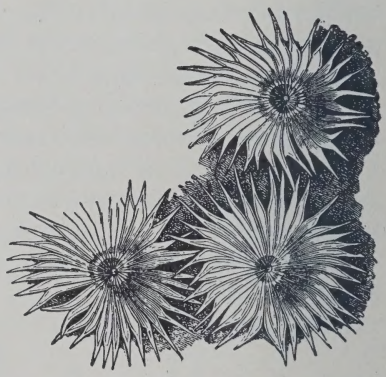


FIG. 43.—Shield-shaped scale-like hairs from leaf of oleaster (*Elaeagnus angustifolia*). ×50 diam. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

mullein is due to numerous, large, branched hairs (Fig. 44). What is the significance of the hairs of the mullein?

The Mesophyll.—The ground tissue cells under the epidermis constitute the mesophyll. These are typical parenchyma cells, having thin, soft, cellulose walls. They are usually rich in chloroplasts. The cells near the upper and lower surfaces usually differ much in shape and arrangement. This is not true, however, in leaves which stand vertically, and which are illuminated equally on both sides.

In the leaf in question, however, the cells beneath the upper epidermis are elongated and stand side by side with their longer axes at right angles

* It may be noted here that the resin of the pine tree is not a product of epidermal structures.

to the surface of the leaf. These are the *palisade* cells (Fig. 39). The palisade tissue may consist of one or more layers of cells. Between the palisade cells and the lower epidermis is the *spongy* parenchyma. These cells are irregularly rounded, so that numerous large intercellular spaces occur between them. The intercellular spaces are in communication with each other, and with the outer air through the stomata. It is apparent that the leaf has two surfaces exposed to the air, an *internal* and an *external* surface. The surfaces of all the cells next to the intercellular spaces constitute the internal surface of the leaf. In certain plants,

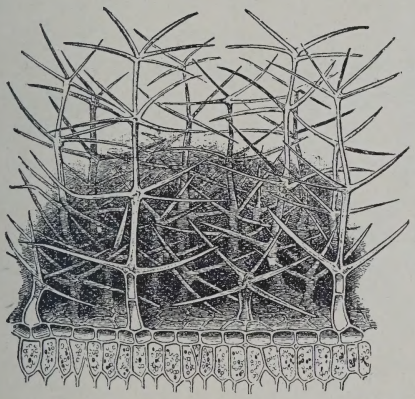


FIG. 44.—Branched hairs from the mullein. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

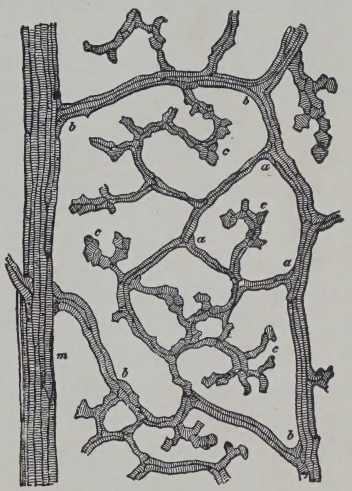


FIG. 45.—A few meshes of the smallest veins of a leaf of Anthyllis; *m*, main vein; *b*, *b*, branches; *a*, *a*, *a*, a closed mesh. The cells of the xylem only are shown; the bundles of bast and the green cells have been omitted. (From Sachs "Lectures on the Physiology of Plants," Clarendon Press.)

e.g., some of the ferns, which grow in the shade and have tender leaves, all of the mesophyll consists of spongy parenchyma.

The vascular system of the leaf make up the veins. The numerous ramifications of the smaller veins anastomose to make an extremely elaborate network (Fig. 45). The veins give support to the leaf blade and transport food and water to and from the leaf. In cross sections of the veins it is readily seen that the wood faces the upper (adaxial) surface, while the bast is turned toward the lower abaxial side (Fig. 39).

The strands of bast in the larger veins of the leaf do not extend to the ultimate extremities of the smallest veinlets. These are surrounded by the *border parenchyma* cells in which chloroplasts may be lacking (Fig. 46).

The border parenchyma serves to conduct the surplus food (sugar) made in the mesophyll to the bast present in the lower reaches of the veins whence the sugar is transported farther into the plant. The wood of the veinlets which reach minute areas of mesophyll cells supply them with water and mineral salts.

Anatomy of the Petiole.—Leaf petioles are very variable in form and structure. They may be cylindrical, flattened, grooved, or variously modified into many forms. The vascular bundles are not arranged in a circle, but appear either in a curve as seen in a cross section of the petiole, or their arrangement may be irregular. The tissues outside of

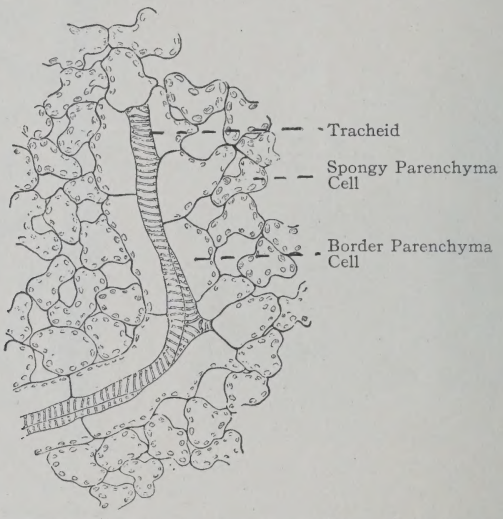


FIG. 46.—The end of a very small veinlet as seen in a section of the spongy parenchyma cut parallel to the leaf surface. The walls of the conducting cells of the veinlet have spiral thickenings. The veinlets are surrounded by the border parenchyma cells which serve to conduct the sugar from the mesophyll to the bast cells of the vein. (Strasburger, Macmillan Co.)

the vascular bundles are similar to those occurring in the cortex of the stem.

Functions of Foliage Leaves.—The three functions of foliage leaves of greatest importance are (1) the manufacture of food from carbon dioxide (CO_2) and water (H_2O), (2) the evaporation of water vapor, and (3) respiration. The first named is known as *photosynthesis* and the second as *transpiration*. It should be remembered, however, that these functions are not confined exclusively to foliage leaves, for any part of the plant possessing chlorophyll may perform the work of photosynthesis and all parts of the plant may evaporate moisture, while every living cell which uses food must carry on respiration. The first two of these functions will

be presented in the paragraphs immediately following, while respiration (energy release) will be taken up in a later chapter.

Photosynthesis.—The "organs" of the cell which are the primary makers of organic material are the chloroplasts or those parts of the living protoplasm containing chlorophyll. The blade of a foliage leaf is a device for displaying many chlorophyll bearing cells to conditions favorable to this food-making process.

For the sake of simplicity we may compare the leaf as well as other green tissue to a manufacturing establishment. The living chloroplasts constitute the machinery; the raw materials used are carbon dioxide and water; and the energy or power necessary is light, either daylight or suitable artificial light. The end product visible to the eye is starch or oil, although sugar may be present before the appearance of starch. Oxygen is the by-product.

The exact manner in which the leaf makes the sugar is only very imperfectly understood. Expressed in chemical terms the process may be indicated as follows:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2.*$$

Now $C_6H_{12}O_6$ is the chemical formula for a molecule of the sugar, glucose. A molecule of carbon dioxide consists of one atom of carbon (C) held in a bond of union with two atoms of oxygen (O). Likewise a molecule of water is a union of two atoms of hydrogen (H) and one atom of oxygen. The chloroplast must first break the bonds of union in these two molecules, that is, the carbon must be separated from the oxygen in the CO_2 molecule, and the bond of union in the water molecule must be loosened. This being accomplished, the chloroplast then combines 6 atoms of carbon, 12 atoms of hydrogen and 6 atoms of oxygen into a molecule of sugar. From the above equation we see that the chloroplast, to secure the proper number of carbon and hydrogen atoms, must use 6 molecules of CO_2 and 6 molecules of H_2O. There is more oxygen in the collection of molecules used than is necessary to make the sugar. The unused oxygen is given off or set free as a *by-product.*

In making sugar, the chloroplasts in the leaf do the work; they build up a complex compound out of simpler compounds. To do this work

* Such expressions as CO_2, H_2O, $C_6H_{12}O_6$ are ways in which chemists indicate the composition of molecules. CO_2 represents a molecule of carbon dioxide which is made of one particle or atom of the chemical element, carbon, and two atoms of the element, oxygen, held in a bond of union. A molecule is the smallest particle in which any substance can be divided and remain that substance. H_2O means that two atoms of hydrogen are held together with one atom of oxygen to make a molecule of water. In a molecule of glucose it takes 6 atoms of carbon, 12 of hydrogen, and 6 of oxygen to make a molecule. If these atoms are separated by breaking their bond of union, they no longer represent glucose.

energy is required, and the energy used in nature is light. The energy necessary, therefore, to run the machinery in the leaf is light.

Source of Raw Materials.—As we have learned, the raw materials necessary for photosynthesis are carbon dioxide and water. The surrounding air is the source of the carbon dioxide, while the water is obtained from the soil. In case the plant is a submerged aquatic the carbon dioxide is derived from that which is dissolved in the water.

Speaking generally we may say that the air, which is a mixture of gases, has approximately the following composition:

Nitrogen	78.1 %
Oxygen	20.8 %
Argon	1.0 %
Carbon dioxide	.03%

Traces of ammonia and other gases.

In order that carbon dioxide may be used by the chloroplasts in the process of photosynthesis this gas must pass into the cells in solution in water. Since all the gases of the air are soluble in water, carbon dioxide passes into cells in solution. The process by which water and substances dissolved in it enter the cell will be explained under the subject of osmosis (page 137).

From the analysis of the air given above, it is evident that any given volume of the atmosphere must contain proportionately a very small quantity of carbon dioxide. At present there are about three liters of carbon dioxide in 10,000 liters of air, or only 2 grams of carbon in 10,000 liters of air. In order, therefore, that a tree having a dry weight of 5,000 kilos (five and one-half tons) may acquire its 2,500 kilos of carbon, it must deprive 12 million cubic meters of air of their carbon. In the light of these facts it was not strange that the discovery of photosynthesis by Ingenhouss was reluctantly accepted, and later rejected and forgotten. The correctness of his discovery was definitely established by the researches of Senebier, De Saussure, and Boussingault. Liebig in Germany was among the first to call attention again to this discovery which today is accepted without question. It must be remembered that a plant makes much more food than is necessary to supply the carbon of its dry weight, since much food is consumed in supplying energy during growth and in reproduction.

Source of Energy in Photosynthesis.—The synthetic process performed by the chloroplasts differs from other synthetic processes (anabolism) not only in the raw materials used, but also in the kind of energy required, which, as stated in the preceding, is normally sunlight. Sunlight, however, is composed of different kinds of light, namely, the seven

primary colors,—violet, indigo, blue, green, yellow, orange, and red. When a beam of light is passed through a prism, the beam is spread out into a band colored like the rainbow. This band is called the *spectrum.* One end of the band shows the red, and the opposite end the blue or violet colors. The different kinds of light are regarded as forms of energy consisting of waves or vibrations. Those at the red end of the spectrum have the longest wave lengths and those at the violet end the shortest.

If sunlight be allowed to pass through an alcoholic solution of chlorophyll then through a prism, it will be found that the spectrum will show two dark bands close together at the red end (between the Fraunhofer lines B and C, Fig. 47) and three broad bands which, in strong solutions, obscure the violet end of the spectrum. These dark bands indicate the rays of light absorbed by the chlorophyll. Experiments have shown that

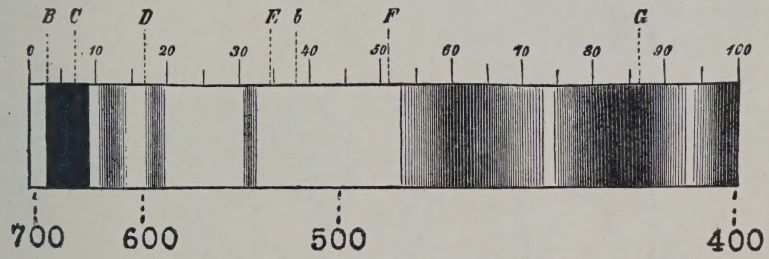


FIG. 47.—Absorption spectrum of an alcoholic solution of chlorophyll from foliage leaves according to G. Kraus. The Fraunhofer lines, B, C, etc., are indicated above and the wave lengths (700–400) below. The black and shaded regions are those where the light has been absorbed or weakened.

the two bands at the red end of the spectrum of sunlight are most efficient as energy in the process of photosynthesis.

An ingenious experiment to demonstrate the effectiveness of certain light rays in photosynthesis, as mentioned in the preceding, was devised by Englemann who used motile bacteria as indicators of the presence of oxygen. An algal filament and motile bacteria were mounted together upon a slide in water. To prevent the diffusion of air into the water of the mount the edges of the cover glass were sealed with vaseline. When the preparation was kept in the dark the bacteria were found to be scattered uniformly in the water, but when the preparation was illuminated the bacteria tended to collect along the filament, owing to the presence of oxygen evolved by the green cells. If the light were cut off, the bacteria would scatter in the water, only to return to the filament again when the preparation was illuminated. Englemann then cast a small spectrum across the field of the microscope by means of a suitable apparatus. The alga was so adjusted that the colors of the minute spectrum succeeded each other along the length of the filament. In a short time the bacteria

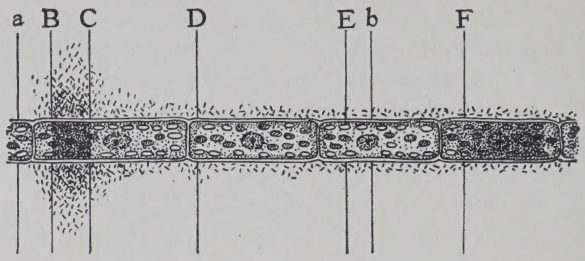


FIG. 48.—Diagram to show the effect of the spectrum upon the evolution of oxygen during photosynthesis in algal cells when bacteria are used as indicators. The largest accumulation of bacteria is seen in the region of the spectrum between lines B and C, the rays which are most efficient in photosynthesis. (Stevens.)

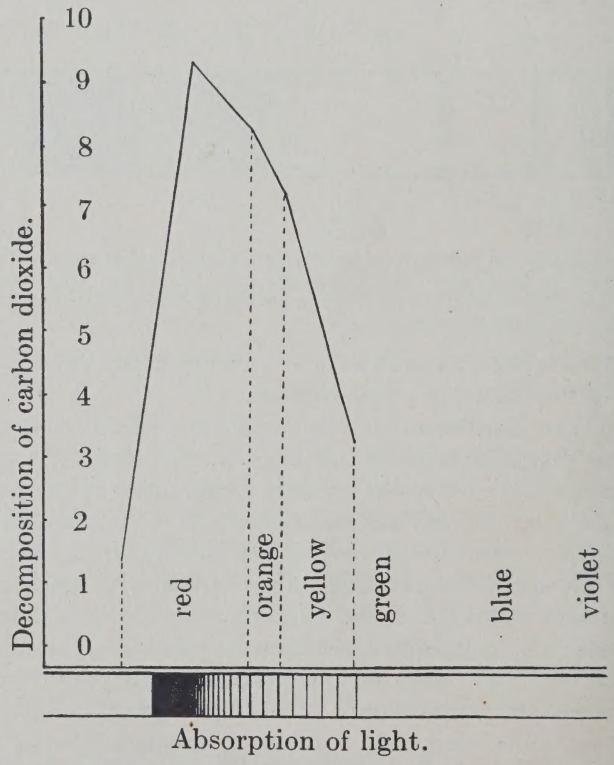


FIG. 49.—Graph illustrating the relation between the portion of the spectrum absorbed by chlorophyll and the portion most efficient in decomposing carbon dioxide. (Adapted from Timiriazeff.)

collected chiefly about the cell or cells illuminated by the red light, thinning out gradually in the orange and yellow, until relatively few were found in the regions of green, blue, and violet (Fig. 48). Inasmuch as the bacteria are very responsive to oxygen, their accumulation near the cells illuminated by the red light showed that the greatest photosynthetic activity took place in the presence of the red rays.

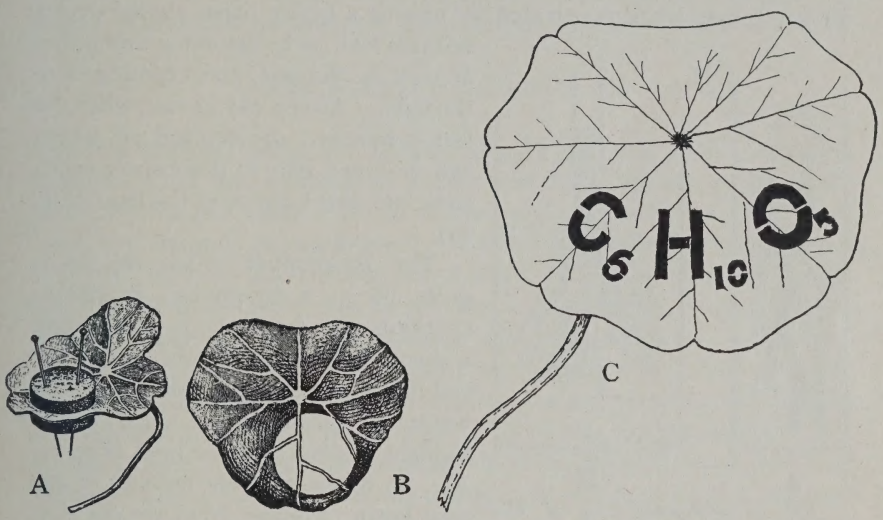


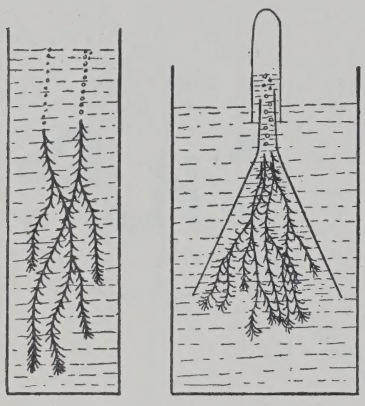
FIG. 50.—Demonstration of the production of starch in illuminated parts of foliage leaves. A, leaf with piece of cork attached which cut off the direct rays of the sun. B, the same leaf decolorized and treated with iodine after removal of cork 24 hours later to show that starch was removed from the shaded spot and not replenished. The illuminated portion turned blue on addition of iodine, an indication of an abundance of starch. C, the entire leaf was shaded except the part indicated by letters CHO.

Timiriazeff has constructed a curve to show graphically the relative quantities of carbon dioxide decomposed by the different parts of the spectrum. In Fig. 49 the highest point of the curve represents the most efficient rays. These have been shown to be the absorption bands in the chlorophyll spectrum which correspond to the red or orange of the solar spectrum; i.e., the bands between the Fraunhofer lines B and C. The rays of light absorbed by the chlorophyll are those that doubtless supply the energy for the work of the chloroplast.

The necessity of light in the process of photosynthesis may be demonstrated by any one of a number of simple experiments. If, from young and vigorous leaves of any suitable plant, the light be excluded by an opaque paper cover for a day or longer, the iodine test will reveal no starch in the blades of the leaves. The starch in the leaves at the beginning of the experiment was removed by a process to be explained in a later paragraph. The cover is now removed, and the leaves exposed to the light. After a

few hours an abundance of starch will be revealed in the leaves by the iodine test. If, instead of a large leaf, some alga, moss plant, or a shoot of Elodea, which has small, thin leaves, be used, a microscopic examination will show that the starch is located in the chloroplasts.

In plants well exposed to the sun the effect of the light seems, however, to be direct, and local, diffuse light being only slightly or not at all effective. This fact may be demonstrated by placing a heavy paper stencil over a suitable leaf, or by fastening thin pieces of cork to the leaf, and exposing it to the light. After a day or two, when the leaf is removed and decolorized, starch will be found only in those spots which have had direct access to the light (Fig. 50).



A B

FIG. 51.—Demonstration of the liberation of oxygen during photosynthesis. A, release of bubbles of oxygen gas from the cut end of the stem of Elodea in sunlight. B, collection of the gas, mainly oxygen, from aquatic plants in sunlight during photosynthesis.

The By-product.—That oxygen is given off as a by-product in photosynthesis may be shown by suspending a shoot of Elodea, with the freshly cut end uppermost, in a glass cylinder of water, and exposing the apparatus to sunlight or good artificial light (Fig. 51, A). In a few minutes bubbles of gas may begin to escape from the cut end. The rapidity with which the bubbles are given off is a fair index of the photosynthetic activity. Furthermore a quantity of Elodea, or some other suitable plant, may be placed in a glass vessel of water under an inverted funnel, over whose stem is suspended an inverted test tube completely filled with water. The gas given off by the plants will collect in the upper end of the tube, displacing the water (Fig. 51, B). A glowing splinter thrust into the tube will indicate the presence of oxygen, by its increased brightness. It can be shown by experiment that the quantity of oxygen given off is approximately equal to the carbon dioxide absorbed

$$\left(\frac{CO_2}{O_2} = 1\right).$$

The Products of Photosynthesis.—In the vast majority of plants the first visible product of photosynthesis is starch. In certain algae, as in the common green felt, Vaucheria, oil is the first visible product. In some monocotylous plants belonging to the banana family, oil is likewise the

first product which can be seen in the cells. In some plants the sugars remain in solution, there being in such cases no visible product. The sugar resulting as the immediate product of photosynthesis is usually glucose ($C_6H_{12}O_6$), but it may also be cane sugar ($C_{12}H_{22}O_{11}$).

The Steps in the Process of Photosynthesis.—The manner in which this comparatively simple chemical process is accomplished, as has been stated, is unknown at present. The reaction may be indicated as follows:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

the free oxygen being the by-product. While this simple equation indicates what may take place, it throws no light on the details of the process. Inasmuch as a molecule of glucose ($C_6H_{12}O_6$) is just six times as large as a molecule of formaldehyde (CH_2O), and as the aldehydes have a tendency to unite into compounds of larger molecules, it is conceivable also that formaldehyde may be condensed into glucose thus: $3CH_2O + 3CH_2O = C_6H_{12}O_6$. The supposition that two or more very simple processes are involved is strengthened by the fact that if Spirogyra, for example, is supplied with formic aldehyde in the absence of carbon dioxide, and exposed to the light, starch may be formed in the chloroplast. If a molecule of water be split off chemically from the glucose, the proportional number of the respective elements will then be the same as in a molecule of starch, $C_6H_{10}O_5$. However starch is a very large molecule and it is written $(C_6H_{10}O_5)_n$.

Conditions Facilitating Photosynthesis.—Generally speaking, it may be mentioned that whatever is necessary for the development of chlorophyll is likewise important in the process of photosynthesis. The formation of chlorophyll proceeds best with suitable light, temperature, oxygen, and the presence of iron. As magnesium is the only mineral element found in chlorophyll, it is highly probable that this element may be necessary, perhaps even more necessary, for the development of chlorophyll than the presence of iron. Chloroplasts function poorly, or not at all, in starved cells.

Considered from a chemical standpoint, one of the most remarkable phenomena in the process of photosynthesis is the fact that it can be carried on in the plant at comparatively low temperatures. The range is from the freezing point (minimum), or a few degrees below, in temperate regions to 43° or 45° C. (maximum) under experimental conditions. The heat intensity most favorable lies between 30° and 37° C. Other conditions being favorable, an increase in the carbon dioxide content of the air up to 10% (the normal air content being .03%) results in an increase of carbohydrate production. With the suitable growing con-

ditions, of heat and moisture, it may be said that the limiting factor in photosynthesis is the carbon dioxide content of the air.

Other Processes of Anabolism.—We may now turn our attention to another class of synthetic activities by which complex carbon compounds are built up in cells. These differ from photosynthesis (1) in that the raw materials used are not carbon dioxide and water, and (2) in that the energy involved is not light, but it comes from within; it is endothermic. The materials, however, are primarily the carbohydrates produced by photosynthesis, while the source and nature of the energy in the cell are very imperfectly understood. These synthetic, or food-making (energy-storing) processes are collectively termed *anabolism*, or *constructive metabolism*.

Probably one of the simplest anabolic processes is the making of starch by the leucoplasts. It was pointed out in a preceding paragraph dealing with the leucoplasts (p. 13) that starch made in the leaf, of the potato plant for example, is changed to glucose by digestion, and transported in solution to the tuber, where the glucose is changed into starch again by the leucoplasts. The change may be expressed thus: $C_6H_{12}O_6$ + action of leucoplasts = $C_6H_{10}O_5 + H_2O$. The expression may seem to indicate that a molecule of starch is simpler than one of glucose, but the starch molecule is a very large one, as stated above, being more properly written $(C_6H_{10}O_5)_n$. This means that the carbon, hydrogen, and oxygen are combined in such a manner that for every six atoms of carbon in the molecule there are ten atoms of hydrogen and five of oxygen. In building starch from glucose the elements of the glucose are separated and recombined. As starch contains less water than glucose, a given weight of starch represents more stored energy than the same weight of glucose, just as anthracite coal represents more energy than the same weight of bituminous coal.

In a similar manner more complex carbon compounds are built up in cells out of the carbohydrates of photosynthesis. Among these may be mentioned oils and fats, such as linseed oil ($C_{57}H_{98}O_6$), castor oil ($C_{57}H_{104}O_9$), olive oil ($C_{57}H_{104}O_6$), and peanut oil ($C_{63}H_{122}O_6$), etc.*

* These oils are built up by the combination of their fatty acids with glycerine, thus:

$3C_{18}H_{32}O_2 + C_3H_8O_3 = C_{57}H_{98}O_6 + 3H_2O$
lineolic acid + glycerine = linseed oil + water

$3C_{18}H_{34}O_3 + C_3H_8O_3 = C_{57}H_{104}O_9 + 3H_2O$
ricineolic acid + glycerine = castor oil + water

$3C_{20}H_{40}O_2 + C_3H_8O_3 = C_{63}H_{122}O_6 + 3H_2O$
arachidic acid + glycerine = peanut oil + water

$3C_{18}H_{34}O_2 + C_3H_8O_3 = C_{57}H_{104}O_6 + 3H_2O$
oleic acid + glycerine = olive oil + water

The molecular formulas of the above oils represent theoretically chemically pure oil. These oils as found in the plant are impure, containing other bodies in connection with the chemically pure oils.

From the foregoing it is seen that oils and fats are complex substances composed of carbon, oxygen, and hydrogen synthesized by the cell from the products of photosynthesis, and that they represent stored food, or stored energy.

Another class of synthesized products exists in what are known as amino-compounds, into whose make-up nitrogen enters, in addition to carbon, oxygen, and hydrogen. As an illustration, amino acetic acid, $CH_2NH_2.COOH$, may be mentioned. Amino acetic acid is derived from acetic acid (CH_3COOH), with one hydrogen atom replaced by the amino radicle,—NH_2.

The nitrogen is not obtained from the photosynthetic product. It is one of seven elements from which, together with carbohydrates, food, tissue-building elements, and protoplasm itself are synthesized by the cells of the plant. These seven elements, nitrogen, potassium, phosphorus, sulphur, calcium, magnesium, and iron, are obtained from the water in which the plant lives, or from the water in the soil upon which the plant grows. (Plants devoid of chloroplasts are not included here.) All of these except nitrogen are frequently referred to as the mineral, or ash, constituents of plants, because they are left in the ash when the plant is burned. The nitrogen is derived from the decomposition of organic matter in the soil; or it is fixed from the air by certain bacteria that form tubercles on the roots of plants of the bean family, and by other soil bacteria.

The mineral elements enumerated above are not accessible to the plant in the free state. With the exception of the bacteria just mentioned, plants cannot utilize the free nitrogen of the air or the free mineral elements in the soil.* All of these elements must be combined with other elements in the form of soluble salts. For example, nitrogen may be accessible when combined with potassium, in the form of potassium nitrate (KNO_3); sulphur and magnesium as magnesium sulphate ($MgSO_4$); iron as iron sulphate ($FeSO_4$), etc.

The mineral salts in themselves do not constitute plant food, as the plant does not secure energy from them as such; but they play an important role in the utilization of food by the plant, and in the building of protoplasm. The several mineral elements probably play different roles in different classes of plants, or in different plants of the same class. Iron is necessary to the formation of chlorophyll in the chloroplast, but this metal is not a constituent of the chlorophyll molecule.

Among other mineral elements found in plants are sodium, chlorine, boron, and silicon. These, while often present, do not seem to be as

* It has been claimed that certain green plants are capable of utilizing the free nitrogen of the air to a very limited extent.

essential as those mentioned in the preceding paragraph. Sodium may aid, in the absence of sufficient potassium. Chlorine is beneficial to such plants as asparagus. Silicon, though present in large quantities in tissues

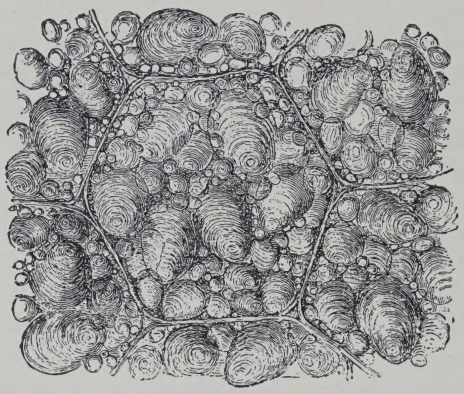


FIG. 52.—A few cells of the white potato filled with storage starch, highly magnified. (From Figurier.)

of corn, other cereals, and scouring rushes, is not known to be of much use to those plants as food elements.

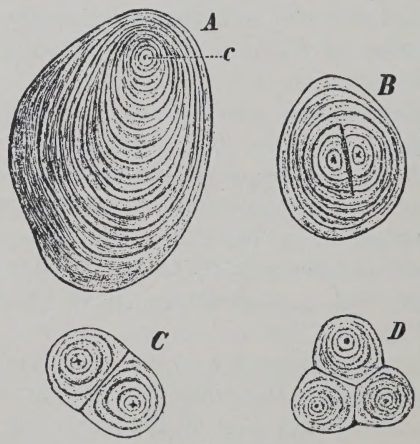


FIG. 53.—Starch grains of the white potato. A, simple grain; B, half compound; C, D, compound grains. *c*, organic center of grain. (Strasburger, Macmillan Co.)

In addition to oils and fats and the amino compounds mentioned above, numerous and much more complex organic substances are synthesized. The nearest to protoplasm, which is in a large measure protein in character, are the protein compounds. The chemical formula for one of the proteins, *zein*, from Indian corn, has been calculated as $C_{736}H_{1161}N_{184}O_{208}S_3$. This and like expressions have very little meaning to anyone but an organic

chemist. What the composition of a molecule of protoplasm is no one knows. It is highly probable that the protoplasmic molecule is more complex than that of any protein, and in active living cells it is undoubtedly a very unstable molecule.

Food Storage.—As already stated, plants produce far more food than they use daily. The surplus is stored as reserve food in leaf, stem, root, or in seeds whence it may be drawn upon for future growth. Leaves, stems, and roots, functioning as storage organs will be commented upon in following chapters.

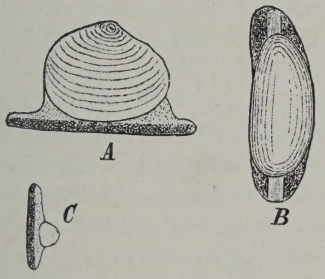


FIG. 54.—Leucoplasts with starch grains from tuber of the orchid *Phajus granifolius*. A, side view; B, from above; C, leucoplast with beginning of starch grain. (Strasburger, Macmillan Co.)

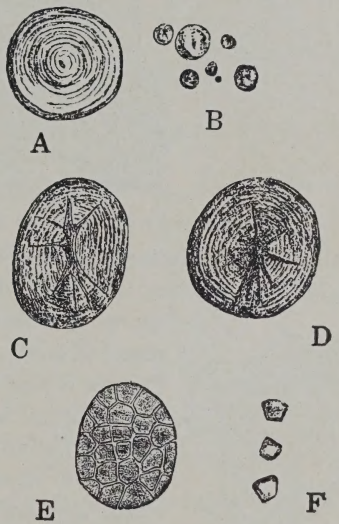


FIG. 55.—Various kinds of starch grains. A, large and B, small starch grains from wheat. C and D, from the bean; E, compound grain from oats; F, parts of the compound grain from oats. (Strasburger, Macmillan Co.)

There are three or four general classes of reserve foods, carbohydrates, fatty oils, amino-compounds and proteins. The carbohydrates consist mainly of starch, sugars, and a form of cellulose, *hemicellulose*. In the root of the Dahlia the carbohydrate, *inulin*, is present. Starch is found in visible granules or grains which may be so numerous that they almost fill the cells, as in the potato (Fig. 52). Each starch grain is a flat disk composed of concentric layers eccentrically arranged (Fig. 53). In its formation by the leucoplast the grain appears first as a small round body about which are added, in regular sequence, the subsequent layers. Starch grains are of various sizes, some of the largest occurring in the

white potato. When two or more grains are formed by a leucoplast, a compound grain results (Figs. 53, 55). The leucoplast is usually small and difficult to recognize, except in certain plants (Fig. 54). Proteins

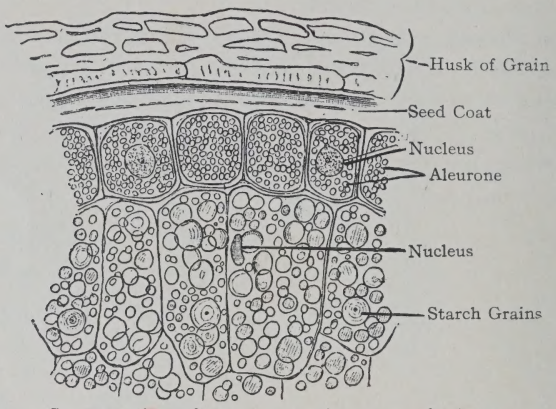


FIG. 56.—Cross section of outer part of a grain of wheat.

occur also in recognizable granules especially in seeds where that class of reserve food is abundant (Fig. 57). In the outer layer of cells of the endosperm of wheat, corn, etc., protein appears in small round granules known as *aleurone* grains (Fig. 56). Protein is also abundant in beans and peas. Below the aleurone layer the cells contain chiefly starch. It may be noted here that fine white flour is made from the starchy endosperm cells of the wheat, while the darker and perhaps more nutritious flour contains the aleurone and other less starchy portions. The large aleurone grains of the castor oil seed contain crystalloids (Fig. 57).

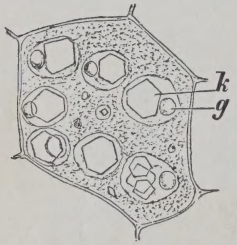


FIG. 57.—A cell from the endosperm of the castor oil plant (Ricinus) containing large protein grains in which are seen a crystalloid *k*, and a globoid *g*. (Strasburger, Macmillan Co.)

Fatty oils such as used for food by man, occur in large quantities in seeds and fruits. The terms cotton seed oil, beech nut oil, linseed oil, olive oil, and maize oil suggest both the plant and the part from which the oil is obtained. Commercial castor oil is obtained from the seed of the castor oil plant (*Ricinus communis*).

Hemicellulose is a modified cellulose, easily digested by the plant, but only in part by animals. It is a part of the thick cell walls in the endosperm of tropical seeds, as in the Date, Ivory Nut, and in other palms. The endosperm of the Ivory Nut is so hard when dry that it is sometimes spoken of as "*vegetable ivory*."

Essential, or aromatic oils, are those which volatilize and produce many odors given off by flowers and other plant parts. They differ much

from the fatty oils. The better known are Clove oil, Cedar oil, oil of Lavender, oil of Orange rind, oil of Lemon, etc. These oils are commonly produced in special cells constituting glands.

Related to the essential oils are the *resins*, *camphor*, and *caoutchouc*, the latter being the basis of *rubber*. Resins (more commonly known as rosin), pitch, balsam, and spruce gum, are formed chiefly in special passages in trees of the pine family. Amber is fossil resin. Camphor is a gum obtained from the camphor tree.

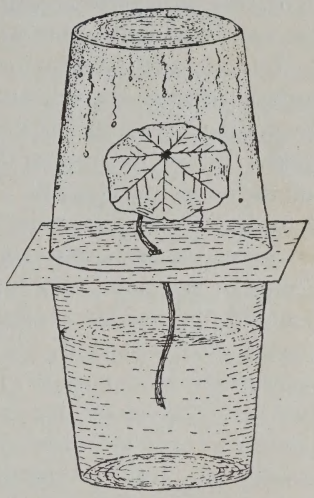


FIG. 58.—Apparatus to demonstrate the evaporation of water vapor from a leaf.

Transpiration.—Another characteristic function of foliage leaves is transpiration or, as stated in a preceding paragraph, the evaporation of water vapor. One may easily convince oneself of this fact by means of a simple experiment. For example, if a leaf of any suitable plant be supported by a piece of stiff paper through which the petiole extends into a glass of water, and then covered by an inverted glass, as shown in Fig. 58, the whole being placed in sunlight, in a few minutes moisture will be visible upon the wall of the inverted glass. In a comparatively short time the condensed moisture will collect in drops and run down the sides of the inverted glass. Foliage leaves are unusually well adapted to the evaporation of water, because (1) of the large surface exposed to the air and direct rays of the sun, (2) of the numerous pores in the lower epidermis and (3), because of the thin tender walls of the cells, especially the cells in the interior of the leaf. The cell surfaces adjacent to the intercellular spaces, or the internal surface of the leaf, evaporate into those spaces moisture which escapes through the numerous stomata when these are open.

The quantity of water evaporated by certain plants is often very great. A large sunflower will evaporate on a warm day over a quart of water. A plant of Indian corn transpires 14 quarts of water during its period of growth (173 days), and a hemp plant 27 quarts in a growing period of 140 days. It has been estimated that a beech tree transpired on an average of 75 quarts of water daily during the summer, while a birch tree possessing about 200,000 leaves evaporated nearly 100 gallons during one hot day. According to calculations an acre of corn plants transpires about 48 tons of water in a day. Calculations tend to show also that for every gram of dry, solid matter produced in some plants, 250,900 grams of water are evaporated.

In short, the process of transpiration takes place in the following manner: the epidermal cell wall exposed to the air loses some of its water by evaporation. By imbibition the wall replenishes its supply from within the cell. The epidermal cell, having lost water, will, by osmosis, replenish its supply from the cell or cells beneath, which are not transpiring, or only at a much slower rate. This process will continue into deeper lying cells until those are reached which are in contact with the xylem of the vascular bundle, from which a constant supply of water is provided.

Our study of leaf structure has shown that the leaf has also an internal surface, namely, the cell surfaces abutting upon the intercellular spaces. From this internal surface evaporation will take place under certain conditions. In the epidermis of the under side of our typical leaf are the many minute pores, the stomata. The number of stomata is surprisingly large. A medium-sized cabbage leaf is provided with about eleven million, and a sunflower leaf with approximately thirteen million. When the pores are open, the moisture in the intercellular spaces escapes, as may be demonstrated by placing bits of cobalt paper, an indicator for moisture, against the lower surface of the leaf. (Cobalt paper, which is blue when dry, becomes rose-colored when moist.) If the pores are closed, very little or no moisture will be given off, the cobalt paper remaining blue. The guard cells are able to open and close the pores under certain conditions. When the stomata are open, transpiration is at its maximum; when they are closed, transpiration sinks to near its zero point. Because of this behavior of the guard cells, the leaf is able to control transpiration to a certain degree. During bright, warm, sunny weather, with a certain degree of humidity in the air, the stomata are wide open; darkness and dry air, on the contrary, tend to close the pores. The wilting frequently observed in broad-leaved plants during the warmer hours of bright, sunny days is due to excessive transpiration. While the water evaporated from the surface of epidermal cells—*cuticular transpiration*—is considerable, the quantity lost by the leaf through *stomatal transpiration* is very much greater.

Not only does the leaf tend to regulate stomatal transpiration in the manner just mentioned, but surface evaporation in general is diminished by the presence of cutin and wax in the outer epidermal walls. The cuticular layers may be so thick that evaporation is scarcely observable. Corky walls act in a manner similar to cuticularized walls. Various fruits, such as apples, pumpkins, melons, and vegetative parts, such as potatoes, etc., remain fresh though severed from the plant, because of the water-proofing of the corky or cuticularized layers. The evaporation of water from the surface of the plant is a physical process that takes place in some degree at all times. While the plant may tend to regulate transpiration, it cannot stop it altogether.

In some cases, as when the relative humidity of the air is low, when the soil is dry, or when the roots of the plant have been disturbed, transpiration may reduce the water content of the plant to a point at which serious injury, or even death, may occur. In fact, the relation between the rate of transpiration and the water supply is the limiting factor of agriculture in many regions otherwise favorable.

Summary of Conditions Affecting the Rate of Transpiration.—All physical conditions which promote rapid evaporation facilitate transpiration. Plants with broad flat surfaces in which the cell walls and the cover of cutin is thin and other water-proofing structures are absent, evaporate moisture rapidly. Evaporation is enhanced also by those conditions which open stomata, such as high temperature and bright sunlight. Wind or air currents produce a drying effect by removing the moist air and bringing drier air to the plant. Conditions of the soil which promote the absorption of water by the roots also facilitate transpiration.

On the other hand, diminished surfaces, thick water-proofing, depressed stomata, darkness or diminished illumination, low temperature, humid air, and dry soil, and whatever diminishes the capacity of the roots to absorb water, tend to check transpiration. Among those plants which have diminished surfaces and heavy water-proofing layers consisting of cutin or thick cell walls of the superficial layers, are the Gymnosperms (Pines, Cedars, etc.) and plants of the desert or dry regions, such as Cacti, Agavas, Yuccas, and many others having a similar structural make-up. Gymnosperms are, as a rule, dry soil plants. Their needle-shaped or scale-like leaves not only have their surfaces reduced to the minimum, but the thick cutin, the thick epidermal cell walls, and depressed stomata tend to check the evaporation of moisture. In some desert plants the stomata are located at considerable distances below the surface at the bottom of narrow canals which may have a zigzag course. From such stomata evaporation takes place much more slowly than from stomata located at the level of the leaf or stem surface.

It is believed that the clothing of hairs upon plants tend to check transpiration. Vertical positions and those by which the edges of the leaves are exposed to the strongest impinging light are also influential in diminishing evaporation.

The Role of Transpiration in the Economy of the Plant.—Transpiration is sometimes styled a "necessary evil," and its importance to the plant constitutes an inviting field for speculation. Explanations have often resolved themselves, however, into purely academic discussions.

Two facts seem to stand out clearly. As will be shown in the chapter dealing with the transportation of fluids in the plant, it can not be denied that transpiration from the leaves is a very important factor in the ascent

of sap, its role being the production of a lifting power or suction upon the column of water extending from the roots to the uppermost extremities of the plant.

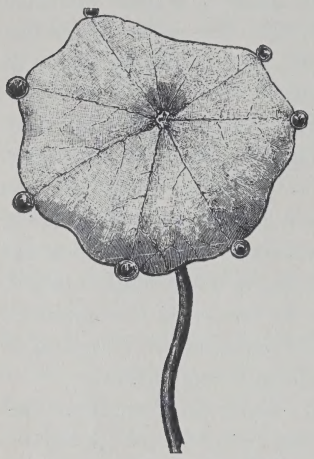


FIG. 59.—Exudation of liquid water at the ends of the large veins of a leaf of the Nasturtium. (Strasburger, Macmillan Co.)

It is clear also that, since the evaporation of water is a cooling process, transpiration must and does have a cooling effect especially upon broad, flat, tender leaves during hot sunny weather. The rise of temperature of such plant parts is considerable, and the cumulative effect would surely result in injury to the tender cells were it not for the cooling effect of evaporation from their surfaces. Experiments tend to show that transpiration reduces the temperature of leaves not to exceed 5° C. yet this reduction is continuous, and the cooling effect may be of greater importance to the leaf than would be indicated by the thermometer.

Exudation of Liquid Water by Leaves.—Not only do leaves continuously throw off water in the form of vapor, but in many leaves liquid water is forced out through the water pores or water glands. This is especially noticeable in the young leaves of many

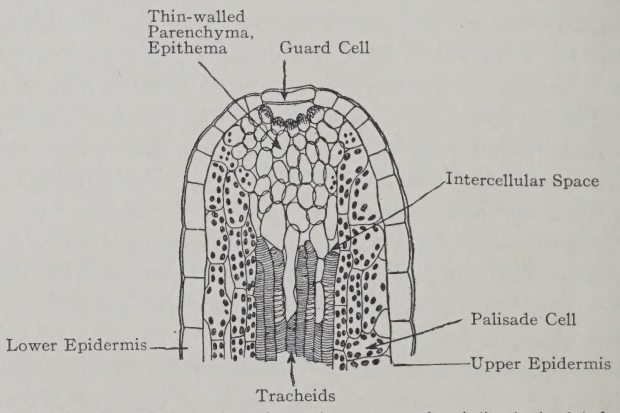


FIG. 60.—Radial longitudinal section through a water gland (hydathode) from the leaf margin of *Primula sinensis*.

plants. To demonstrate this fact all that is necessary is to enclose in a moist chamber a small potted plant of the dwarf Nasturtium or some seedlings of Indian corn. After a few hours, clear drops

of water will be seen hanging from the edge of the younger leaves at the ends of the large veins (Fig. 59), or from the tips of the young blades of corn. Or in early morning, following a still, clear night, similar drops may be observed on the leaves of plants in the open, such as tender blades of grass, young leaves of the grape vine, etc. This water is exuded by peculiar structures between the ends of the veins and the epidermis, known as the *epithema*. The epithema consists of living cells in which the tracheids terminate. In the overlying epidermis are peculiar pores called water pores, or water stomata, (Fig. 60). The water pores

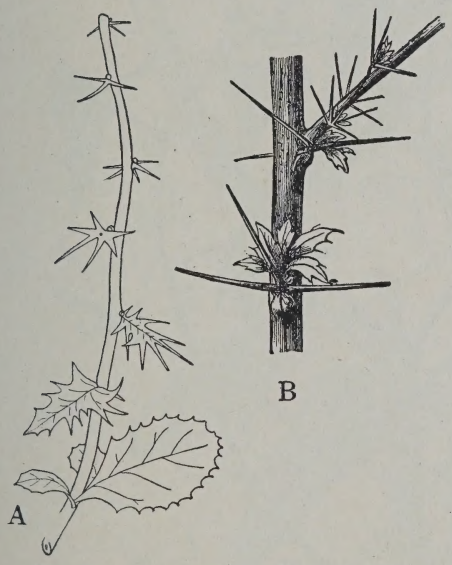


FIG. 61.—A, summer shoot of Barberry, showing transition from leaf to spine. B, shoots have developed in the axils of the three-pointed spines. (B, after Kerner "Natural History of Plants," A. Blackie & Son, Ltd.)

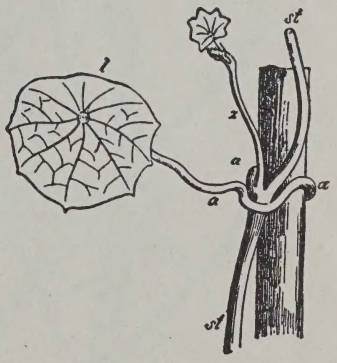


FIG. 62.—Portion of stem of Nasturtium with leaf tendril. The long petiole, *a*, *a*, *a*, of the leaf, *l*, has coiled about the support and its own stem. (From Sachs' "Lectures on the Physiology of Plants," Clarendon Press.)

are much larger than ordinary stomata, and their guard cells keep the pores permanently open. The water exuded frequently contains, among other substances, calcium carbonate, which may remain as an incrustation over the water pores.

It is possible that in submerged water plants exudation may function in the same manner as transpiration in maintaining the current from the absorbing organs.

Modified Leaves and Their Special Functions.—In addition to the two functions, photosynthesis and transpiration, of ordinary foliage leaves,

there are certain other functions which are performed by specialized leaves. The following paragraphs will deal with some of these leaves and the work they accomplish.

Scale Leaves.—Of the commonest and most wide-spread modifications are the scale leaves, occurring as the bud scales of winter buds, and often upon underground stems. Bud scales of woody plants are usually the dry, membranous or corky structures which afford protection to the

FIG. 63.—A portion of Smilax showing tendrils which are modified stipules. Note the manner in which the tendrils cling and shorten. (After Kerner "Natural History of Plants," A. Blackie & Son, Ltd.)

tender parts of the bud within. Their chief role is that of water-proofing and protection against sudden changes of temperature. Bud scales are often provided on the inner surface with a coating of soft, silky hairs, as in some hickories and in the horse chestnut. These scales do not prevent freezing, for buds freeze solid in zero weather. Freezing and thawing constitute a drying process. Freezing brings the water out of the cells where it becomes ice. When the ice melts, the water would evaporate before the tender living parts could again absorb it were it not for the protection afforded by water-proof scales.

Bud scales represent different parts of the leaf in different plants. In some, the scale is a modified blade; in others, the petiole or base. The bud scales of the tulip tree are modified stipules. It may be pointed out here that the adult foliage leaves of the Red Cedar (Juniper) and of the Arbor-Vitae are scale-like.

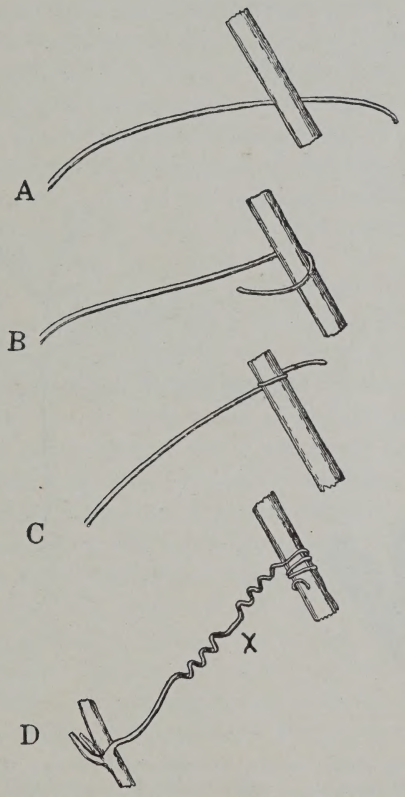


FIG. 64.—Stages in the twining of a tendril of Bryonia. The upper figure, A, represents the first step; in the lower, D, *X* is the point of reversal. In some plants, as in the wild cucumber (*Sicyos angulatus*) the first two stages may take place, in hot weather, in a few minutes; the tendrils in that plant will wind around a pencil or one's little finger if held against the end of the tendril after stroking it gently on the under side. (From Ganong's "Textbook of Botany," Macmillan Co.)

Spines.—The spine is another form of modified leaf. In the barberry, the entire leaf is changed in development into a spine (Fig. 61). The spines at the base of the compound leaves of the common or black locust are modified stipules. The stickers of the cactus are chiefly modified stems.

Like the sharp extremities of other plant parts they serve as organs of defense, and play a useful role in keeping away browsing animals.

Leaf Tendrils.—Another function performed by leaves is that of support. In some climbing plants certain leaves or parts of the leaf are

FIG. 65.—A portion of the stem of Bryony (Bryonia). B, bearing a tendril which is attached to the support, A, by coiling around it; *u*, the straight portion of the tendril; that part of the tendril between *u* and *x* has become changed by growth into a spiral which reverses the direction of the coils at *w*, and *w'*. (Palladin.)

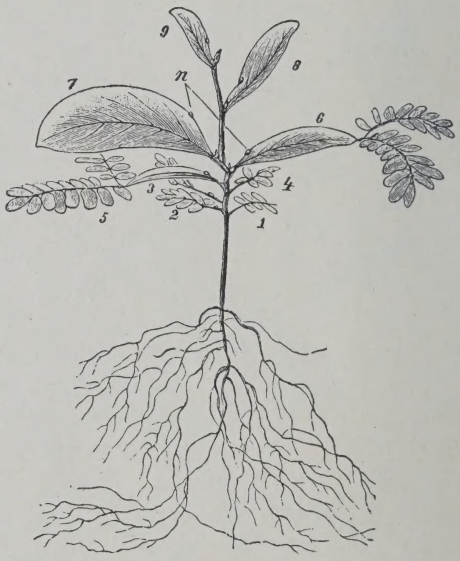


FIG. 66.—Plantlet of *Acacia pycnantha*, showing the development of the leaf petiole into broad blade-like expansions, *phyllodia*, and the absence of the pinnate blades of the older leaves. Leaves 1, 2, 4 have ordinary petioles; 3 and 6 show transition of petiole into phyllodia; 7, 8, 9, phyllodia of older leaves in which the blades did not develop; *n*, nectaries. (Strasburger, Macmillan Co.)

developed as tendrils, slender and thread-like structures which are able to twine around supports of suitable size. A simple case is that of the Nasturtium leaf in which the twining organ, when present, is the petiole, as shown in Fig. 62. In the garden pea (Fig. 21, B, page 33), one or more

leaflets may develop as tendrils. The tendrils of the Smilax are modified stipules (Fig. 63).

The manner in which a tendril, winds around a support is the same whether it be a leaf tendril or stem tendril. When the end of the tendril touches the support it begins to curve. Growth in length and curving continues until one or more complete turns are made. The tendril grows around the support, as shown in Fig. 64, A, B, C, D. The tendril can curve around the support only when it elongates faster on the opposite side than on the side next to the support. The end of the tendril having become attached, the free portion shortens by coiling spirally like a corkscrew, thus drawing the stem closer to the support. The coiling is also a process of growth. For purely mechanical reasons the tendril coils partly to the right and partly to the left. Points of reversal (Fig. 65, *w*) occur between the right and left spirals.

Phyllodia.—Still more instructive perhaps are the leaf modifications of certain Australian Acacias in which the leaf-stalks become modified to do the work of the leaf blades (Fig. 66). In the young plant the first leaves are pinnately compound, but in those developed later the blades become reduced and finally suppressed, while the petiole develops into a broad expansion which takes on the function of a foliage blade.

Leaves of Sensitive Plants.—A very remarkable behavior is found in the sensitive plants. Perhaps the most familiar example is *Mimosa pudica*, a leguminose plant, which may be readily grown in the garden or hot house. In the tropics, its native home, *Mimosa pudica* is a shrubby plant, which is somewhat spiny and which is noted for the peculiar behavior of the leaves when shocked or injured (Fig. 67). The leaves are doubly compound. The four secondary leaf-stalks, bearing each two rows of small leaflets right and left, spring from the end of the primary leaf-stalk. At the bases of the primary and secondary leaf-stalks and of the small leaflets, are motile organs, *pulvini* (sing. pulvinus). All these different parts are capable of independent movements. If, when in the expanded condition (Fig. 67, A) in the daytime, the stem or a leaflet be given a shock, or be injured by a burning match or a drop of acid, the tiny leaflets will immediately and quickly close up bringing their upper surfaces nearly or quite in contact, and at the same time the primary leaf will drop to a downwardly inclined position, as in Fig. 67, B.

The motile organ, the pulvinus, works as follows: when a shock is received, the cell sap in the cells of the lower side escapes from those cells and they become flaccid. The distended cells of the upper side elongate so that that side becomes longer as the lower side shortens, and a hinge action results. Recovery is brought about when the cells of the lower side of the pulvinus become again turgid, by the taking in of the cell

sap. The primary leaf-stalk rises and the leaflets spread out horizontally again.

The leaves perform slowly in the same manner each evening to assume the night position (Fig. 67, B), recovering in the day. The night

FIG. 67.—Parts of two sensitive plants (Mimosa). A, daylight position, the leaves and leaflets are expanded. B, night position, or after stimulation, the leaflets folded together and the leaves dropping. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

position will be assumed during the daytime if the air becomes cool or if the plants be placed in the dark.

The question arises: do these movements enable the plant to adjust itself better to its surroundings? The night position here has the same value as in the case of the night position of other leaves, such as those of the clover (Fig. 35), but the sudden movement induced by a shock or other stimulus is not so easily explained. It was stated above that the

plant is spiny. When the leaves drop and fold into the night position, the nose of a browsing animal is more likely to come in contact with the sharp spines.

Leaves of Insectivorous Plants.—Of special interest also are the leaves of those plants which are able to capture and digest insects. Of these, two are native to Indiana, the Sun-dew (*Drosera rotundifolia*) and the Pitcher Plant (*Sarracenia purpurea*). Both grow in our peat bogs (Figs. 68, 69). The leaves of Drosera are provided with numerous gland-tipped emergences, or "tentacles." If a small insect alights upon a leaf that is neither too young nor too old, it will be held by the sticky substance of the glands, and in the meantime the tentacles will close over the animal

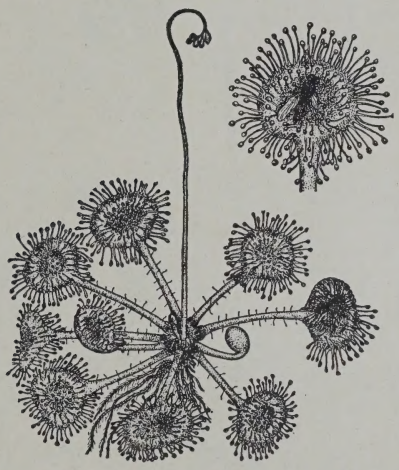


FIG. 68.—*Drosera rotundifolia;* natural size. Above at the right, a leaf showing methods of capturing and holding insects. (From Ganong's "Textbook of Botany," Macmillan Co.)

making escape impossible (Fig. 68, right and above). The secretion of the glands contains in addition to an acid, a peptonizing enzyme which digests the soluble parts of the insect's body. The digested substances and the secretion itself are then absorbed by the leaves. Drosera is easily kept alive in a moist chamber in the laboratory, where the fate of small insects, such as the larvae of the cabbage butterfly, or small bits of the white of a hard boiled egg may be observed from day to day.

The pitcher plant (Fig. 69) has leaves changed into deep reservoirs partly filled with water. Insects that fall or slip in cannot escape, and the soluble juices are digested and absorbed.

These two remarkable plants are likely to become extinct unless present and coming generations are sufficiently interested to provide for their preservation. Very interesting and ornamental pitcher-plants (Nepen-

thes) are cultivated in large conservatories. The leaves of some species serve as a photosynthetic organ, an insect trap, and a tendril (Fig. 70).

Another remarkable kind of insectivorous plant is the Venus fly-trap (*Dionaea muscipula*) (Fig. 71). The leaf blades are sensitive to contact and close rather quickly if touched on the upper side, especially if a

FIG. 69.—Pitcher Plant (*Sarracenia purpurea*). (Reduced from Barton's Elements of Botany, 1804.)

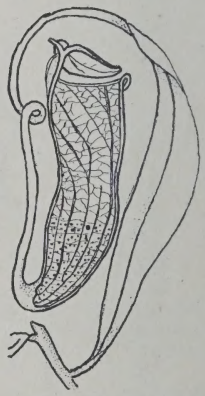


FIG. 70.—Leaf of Nepenthes; foliage leaf, tendril and pitcher (insect trap) combined

bristle be disturbed. A small insect walking upon the leaf is likely to be held and digested. The petioles of the leaves are broadened into phyllodia-like structures.

The Bladderwort, Utricularia.—Turning now to ponds, lakes and marshy places we find the delicate aquatic or marsh plant, Utricularia, some of whose leaf-segments are developed as small, rounded traps, while others are finely divided (Fig. 72). The plant body is submerged, but the flowers open above the surface of the water.

The trap is a bladder-like structure filled with water, whose entrance is fitted with a small valve, or door, opening inwardly which permits the entrance of small aquatic animals but not their escape (Fig. 73). Projecting from the lower margin of the door are four hairs or bristles, the trip hairs. If small animals come in contact with these hairs or with the door itself, the door will open suddenly and some water together with the animals will be drawn into the trap by a kind of gulping movement. The

FIG. 71.—Venus Fly-trap (*Donaea muscipula*), a plant which catches insects by a sudden closing of the leaf blades. Note the rosette habit of the leaves. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

door springs back closing the opening, and the animals are imprisoned. Before the door was sprung the trap was less distended. The inrush of water causes the trap to become more distended. The pressure of the water from within upon the water-tight door keeps it closed. Unable to escape, the animals die and their bodies are digested.

Leaves as Organs of Vegetative Propagation.—The special functions of leaves mentioned in the foregoing pertain to protection, support, and nutrition. Another kind of special adaptation is that of propagation.

Of the two illustrations selected, one pertains to a seed plant, Bryophyllum, and the other to a fern. If a leaf of Bryophyllum be placed upon

FIG. 72.—A Bladderwort (*Utricularia grafiana*). Some branches bear finely divided leaves, and others bladders, insect traps. This plant lives in the water, but raises its flowers up into the air. About two-thirds natural size. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

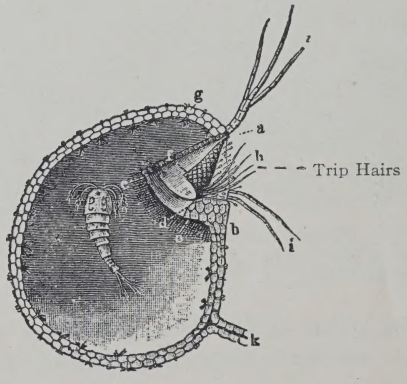


FIG. 73.—Leaf, insect trap, of *Utricularia vulgaris*, halved lengthwise with an imprisoned insect, *Cyclops; a* to *b*, opening with trip hairs, *h*, about it; *b* to *c*, cushion-like rim upon which valve rests, opening inward only; *g*, wall of the leaf with glandular and absorbing hairs. Magnified about 20 diam. (After Cohn.)

earth, which is not allowed to remain too dry or upon moist sand, in a few weeks small plants will arise at the margins from adventitious buds

formed at the ends of the veins (Fig. 74). This is the principal method by which this plant is propagated in the laboratory. *Bryophyllum*

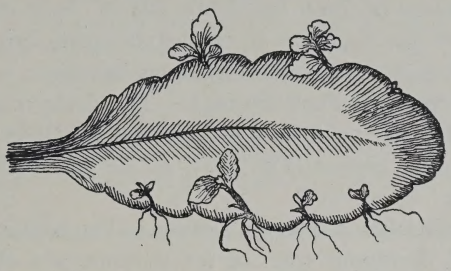


FIG. 74.—Leaf of *Bryophyllum calycinum* showings mall plants developing from the margin.

FIG. 75.—The Walking Fern (*Camptosorus rhizophyllus*). New plants are developing from the tips of the leaves.

calycinum is very hardy and lends itself to many kinds of experimentation. Because of its hardiness it has been called the "life plant."

Very interesting and instructive is the walking fern, *Camptosorus rhizophyllus*, whose leaves take root at the tips when in contact with the

earth or surrounding moss (Fig. 75). This small fern may be found growing upon limestone ledges where only a small quantity of soil accumulates in cracks or crannies or upon the debris left by decaying moss. At the tip of the slender tapering ends of the leaves small fern buds arise from which roots, leaves, and the small stem soon develop.

Leaves as Organs of Food Storage.—The fleshy scale leaves of the bulb of Onion, Tulip, Hyacinth, and Lilies are modified leaf bases developed as food storage organs (Fig. 122), as are also such leaves as those making up a head of cabbage.

Autumnal Coloration of Foliage Leaves.—The brilliant color assumed by the leaves of deciduous trees in the autumn is a distinctive feature of our wooded landscape. The beauty of the forest resulting from the variety and brilliance of colors can be neither adequately described in words nor portrayed in color upon canvas. The dominant yellows of the hard maples and tulip trees, the crimson and scarlet of dogwood, sumac and sour gum, the delicate purples of oaks, the browns of the beeches, and all intermingled with various shades of red, make up the kaleidoscopic panorama which changes from day to day.

When the leaves are mature at the end of the season, the larger part of the remaining food passes into the stem. The chlorophyll green may disappear leaving the chlorophyll yellows, or a more complete decomposition of chlorophyll and the remaining food may result in red and blue pigments (*anthocyanins*). These may be taken up by the cell walls and, if the leaves be dried, they may retain the colors for some months if kept away from direct sunlight.

The browns of the beeches and oaks seem to be due in a large measure to the presence of tannins.

Summary.—Beginning with the two main functions of the leaf, photosynthesis and transpiration, make a table or summary of all the special functions of leaves commented upon in the foregoing paragraphs.

TOPICS FOR REVIEW AND DISCUSSION

Name all the parts which may be present in a leaf.
Classify leaves as to veining, as to margin, as to base, and as to apex.
Distinguish between simple and compound leaves.
What led Linné (Linnaeus) to refer to certain leaves as equitant leaves?
How does light affect the position and arrangement of leaves upon the stem?
What are compass plants?
What is meant by the day and night position of leaves?
What significance have these positions in the economy of the plant?
What are leaf mosaics? In your opinion is the name fitting?
What is the significance of long and short petioles on the same plant?
Where do leaves originate upon the stem? Do leaves spring directly from roots?
In what plants do the leaves continue to grow at the tip until the adult stage is reached?

In leaves of many plants the tip stops growing before the adult size is reached. Where does the growth continue?

What functions do you attribute to the veins of the leaves?

In what respects does the upper epidermis differ from the lower?

Distinguish between *stoma* and *guard cells*.

What are trichomes or epidermal hairs? Enumerate all the kinds of hairs you know.

What role do hairs play in the economy of the plant?

Are glandular hairs of special value to the plant?

Are waxy secretions of any value to the plant? Cite facts in support of your conclusions.

To what is the silvery appearance of such plants as the garden sage, oleaster, sage brush of the desert, etc., due?

Are the hairs of the mullein of any value to the plant?

How does the palisade parenchyma differ from the spongy parenchyma?

In what sorts of leaves is the palisade tissue well developed?

What kind of leaves have palisade cells beneath both surfaces?

In what leaves is the palisade parenchyma absent?

What will happen if plants which grow in shade are brought into strong sunlight?

What are the functions of foliage leaves?

What sorts of leaves do not carry on photosynthesis?

Is the air a chemical compound or a mixture of gases?

What per cent. of the air is carbon dioxide?

About how much air is required to supply 2 grams of carbon?

Who was among the first to discover the process of photosynthesis? Was the process always known by that name? Why was the discoverer's conclusion discredited for so long a time?

Discuss photosynthesis from the standpoint of the necessary energy, light.

Who were Senebier, De Saussure, Boussingault, and Liebig?

Will an increase in the carbon dioxide of the air enable the plant to do more photosynthetic work? What happens if the quantity in the air exceeds a certain per cent.?

Enumerate all the conditions unfavorable to photosynthesis. All the favorable conditions.

How may you know that photosynthesis is going on in Elodea without making any chemical test?

How does the carbon dioxide get into the cells?

What is the by-product of photosynthesis? What is a by-product?

From what does the plant make oils and fats?

Sugar and pure castor oil are composed of carbon, hydrogen and oxygen. How do you account for the difference between the two?

Do leaves make more starch than they use? If so, what becomes of the surplus?

In what two forms is water given off by leaves. Name the two processes involved.

Why do broad leaves evaporate more water from the lower than from the upper surface?

What constitutes the internal surface of the leaf? How does moisture from the internal surface escape into the outer atmosphere?

What environic conditions favor transpiration and what tend to diminish evaporation?

How do plants conserve the water in their tissues? Enumerate fully.

A pine tree will transpire less water than a maple tree. Why?

Leaves of Indian corn and other grasses may roll or curl in hot dry weather. What enables them to roll while leaves of some other plants will merely hang limp under like conditions? Is the rolling beneficial to the plant? Give reason for your answer.

Why do leaves of Rhododendrons suffer more from transpiration when the ground is frozen?

Under what circumstances is transpiration injurious to the plant?

In what respects is transpiration useful? Discuss to the fullest extent of your present knowledge.

Do deciduous trees evaporate moisture in the winter?

Is there any relation between transpiration and the quantity of photosynthetic work done by leaves or stems?

Why has transpiration been referred to as a necessary evil?

Contrast the food making ability of plants in the Amazon valley with that of plants in Arizona. Is transpiration in any way responsible for the difference?

Does transpiration occur in submerged aquatics?

Does water escape from submerged aquatic plants?

What is the function of the epithema?

What are modified leaves? Enumerate all the kinds referred to in the text.

Explain why freezing and thawing constitute a drying process.

May one part of the leaf be modified to perform one function while other parts undergo different modifications which serve other purposes? Cite all the illustrations you know.

The leaves of what plants capture insects and derive food from that source?

Is the behavior of the leaves of the sensitive plant (Mimosa) of any value to the plant?

How do leaves function as organs of vegetative propagation? Cite instances.

Name all the plants you know whose leaves are organs of food storage.

What enables a tendril to wind about a support?

What enables a tendril to make spiral-like coils?

How do water stomata differ from ordinary stomata?

What are phyllodia?

How well is the photosynthetic tissue provided with veinlets? What is meant by border parenchyma in a leaf?

What are succulent leaves?

Why do the epidermal cells of leaves exposed to sunlight have little or no chlorophyll?

Why do leaves standing vertically have palisade cells beneath the epidermis of both flat surfaces?

Are dust and soot injurious to leaves?

Why does washing the surface of leaves of hot house plants improve their vigor?

Does it seem reasonable to you that any tree could evaporate one hundred gallons of water in a day?

Why will slightly frosted plants more readily recover if kept cool and sprinkled?

In what plants do the stems assume the functions of foliage leaves?

What parts of a leaf may become tendrils? Spines?

Explain the autumnal coloration of leaves.

The dropping of leaves in the autumn may be referred to as the *great death.* Why? What would you call the *great birth?*

CHAPTER IV

THE STEM

As stated in Chapter I, stems bear leaves, roots, flowers and fruit. As a rule, the stem ends in a bud which contains the growing point of embryonic tissue from which leaves and new buds arise (Fig. 76). The growing point as seen with the microscope is shown in Fig. 36. As will be pointed out in a later paragraph the cambium is also embryonic tissue.

We may begin the study of the stem with a branch of some woody plant in the winter condition, such as the buckeye, horse-chestnut, or hickory, which possesses scaly buds (Fig. 77). At the end of the stem is the large terminal bud. At intervals upon the stem are large conspicuous areas,

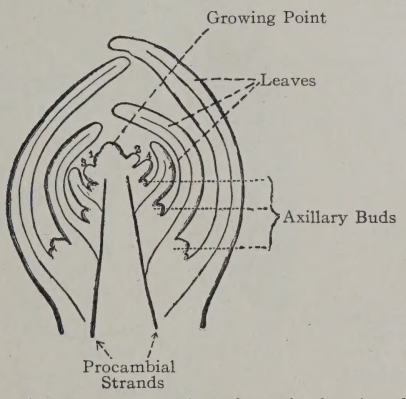


FIG. 76.—Diagram of a longitudinal section through the tip of a stem. 1, 2, 3, 4, successively older beginnings (primordia) of leaves.

leaf-scars, indicating the places, *nodes*, at which the fallen leaves were attached. Arranged in a curved line in the leaf-scar may be seen the ends of the several veins which passed from the leaf into the stem. Above each leaf-scar is an axillary bud. The fine lines encircling the stem are the scars left by the terminal bud scales of the preceding year. That part of the stem between the terminal bud and the scale-scars represents one year's growth.

Scattered over the surface of the stem are small pustule-like protuberances, the *lenticels*. The branches of trees and bushes which are grayish or brownish in color owe their appearance to the dead epidermis and to

the presence of a layer of cork beneath. Lenticels are porous places in the cork, developed usually beneath stomata, which form passages, in the younger branches, for the exchange of gases between the outer air and the live cells beneath the cork. Twigs and branches which remain green in external appearance for a year or longer owe that color to the fact that the epidermis remained alive longer and the corky layer, if present, was late in developing.

The Fall of Leaves.—The trim leaf-scars, so conspicuous by their light brown color in the autumn merit special consideration. Leaves, of such trees as the above, fall from the branch because of a special process of growth. With the approach of autumn, there is formed beneath the leaf base a layer of cork

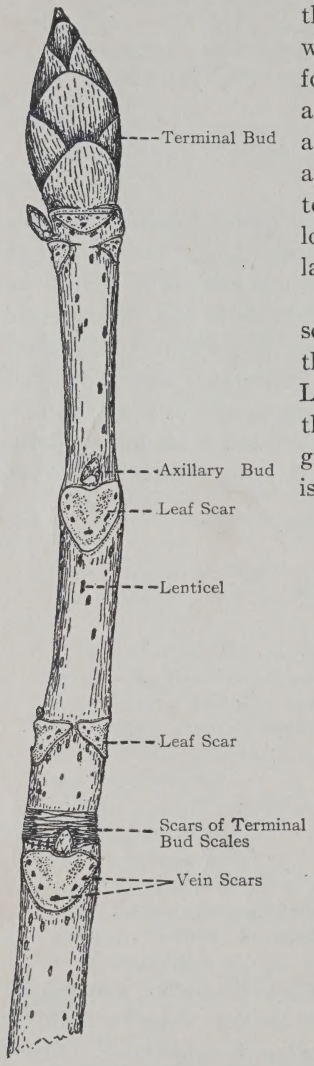


FIG. 77.—End of a branch of the horse-chestnut (*Aesculus hippocastanum*) in the winter condition.

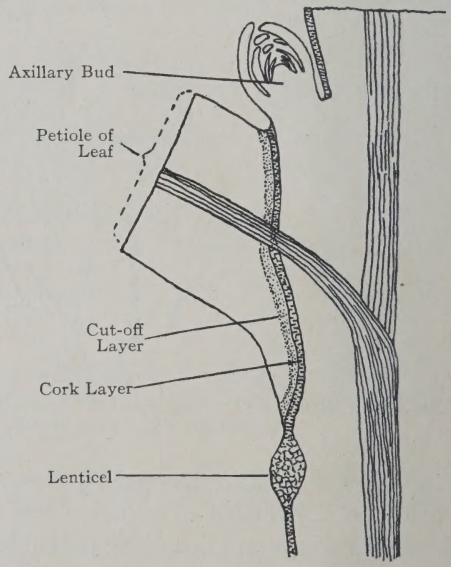


FIG. 78.—Longitudinal section through the base of a leaf and a portion of the stem of the horse-chestnut (*Aesculus hippocastanum*) to which it is attached, illustrating method of leaf fall. (Adapted from F. O. Bower's "Botany of the Living Plant." By permission of the Macmillan Company, Ltd. Publishers.)

which affords protection to the live cells beneath. In the meantime a layer of specially developed cells, the *absciss* or *cut-off layer*,

is formed beneath the outer part of the cork and the base of the leaf. The cells of the cut-off layer remain tender, permitting the leaf to fall of its own weight (Fig. 78). After a frosty night, especially following a rain, the leaves drop readily the next morning. The water, taken up by

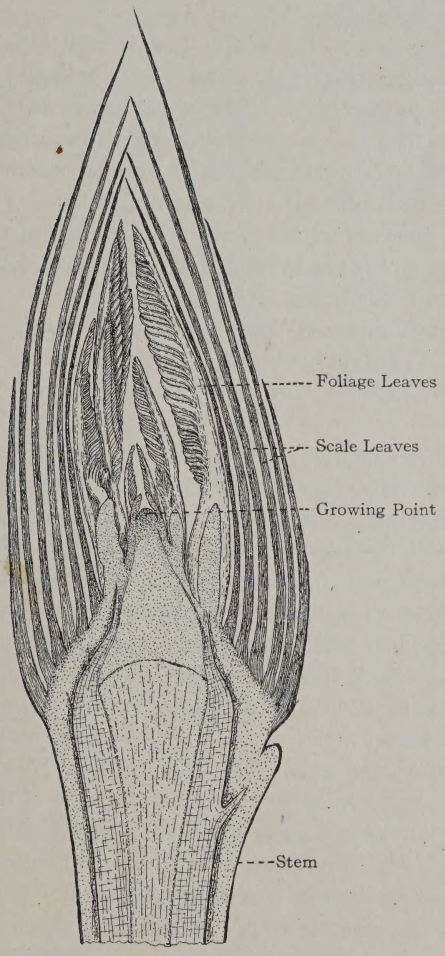


FIG. 79.—Longitudinal section through a terminal bud of the Shellbark Hickory (*Carya ovata* (Mill.) K. Koch.

the cells between the cork layer and the leaf base, freezes, and the resulting expansion severs the connection, so that the leaf drops as soon as the ice melts or sometimes sooner. The veins are chiefly pinched in two by the formation of the cork and absciss layers.

It must be borne in mind, however, that the leaves of all trees do not fall as a result of the process just described. In many cases there is no separating or cut-off layer developed. The leaves die, dry up, and may remain attached to the twigs for a longer time, or during the winter, falling only when the buds begin to expand in the spring. Examples are to be found among beeches and oaks.

Buds.—The structure of a winter bud is well illustrated by that of the shellbark hickory (Fig. 79). The young foliage leaves are covered by the dry, overlapping scales. The young leaves are often covered with numerous hairs. The bud scales may also be provided with a coating of hairs on the inner surface and externally by waxy secretions.

Classification of Buds.—Buds may be classified, (1) as to parts contained, (2) as to position on the stem, (3) as to arrangement on the stem, (4) as to covering, and (5) as to condition and time of activity. Buds may be classified upon other bases.

1. As to parts contained, buds are known as *leaf*, *flower*, and *mixed* buds. A leaf bud contains young leaves only; a flower bud contains one or more unopened flowers; and a mixed bud contains both flowers and leaves.

2. As to position on the stem, buds are *terminal* and *lateral*. A bud which ends a stem of an appreciable length is a terminal bud. Lateral buds are those having a lateral position, or that spring from the side of the stem. Lateral buds are *axillary*, *accessory* or supernumerary, *sub-petiolar*, and *adventitious*. Axillary buds arise in the axils of the leaves. Accessory buds arise at the sides or above an axillary bud (Fig. 80, A, B). They are developed in addition to the regular axillary buds. If placed above the axillary bud, they are called *superposed* buds (Fig. 80, B); if at the sides of axillary buds, they are known as *collateral* buds, as in the red maple (*Acer rubrum*) (Fig. 80, A). Sub-petiolar buds develop beneath the bases of the leaves, as in the sycamore tree. A sub-petiolar bud is really an axillary bud which is covered by the base of the leaf. Adventitious buds arise anywhere upon the plant out of the ordinary positions just mentioned. Attention has already been directed to the adventitious buds formed at the margins of the leaf of Bryophyllum, and at the tip of the leaf of the walking fern, Camptosorus (Figs. 74, 75).

3. As to arrangement, buds like leaves are *alternate*, *opposite*, or *verticillate* (in circles).

4. As to covering, buds are *scaly* or *naked*. Dry, scaly buds are provided with dry, membranous or corky scales. In fleshy buds the scales are sappy or succulent. Naked buds are not protected by dry, corky scales. They occur on some woody plants, as our walnut and sumac, upon plants in tropical rain-forests, and on almost all herbaceous plants.

5. As to condition we may speak of buds as *active*, *dormant*, and *latent*. On young, growing stems buds are in a continuous process of growth and formation. A dormant bud is one at rest or in a non-growing or dormant condition, such as the winter buds of deciduous or evergreen trees and bushes. Latent buds are those which remain undeveloped until something in the life of the plant stimulates them to become active, even though

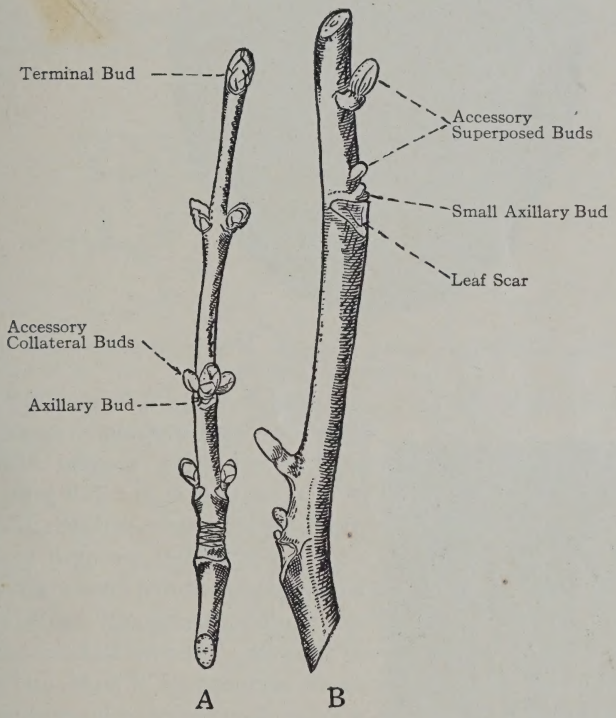


FIG. 80.—A, twig of red maple with accessory collateral buds at the right and left of axillary buds. B, twig of butternut.

they become covered by successive layers of tissue. The axillary bud in the walnut is a latent bud.

The Structure of the Stem.—In presenting the structure of stems the following types will be considered: (1) the type of dicotylous* plants and gymnosperms, (2) the monocotylous stem, and (3) the stem of the fern. For pedagogical reasons and because of its simpler structure, we shall begin with the monocotylous type of stem, using that of Indian corn.

* The terms dicotylous, dicotyledonous, and dicot are synonymous as are also monocotylous, monocotyledonous and monocot.

Stem of Indian Corn.—A cross section of an internode of the corn

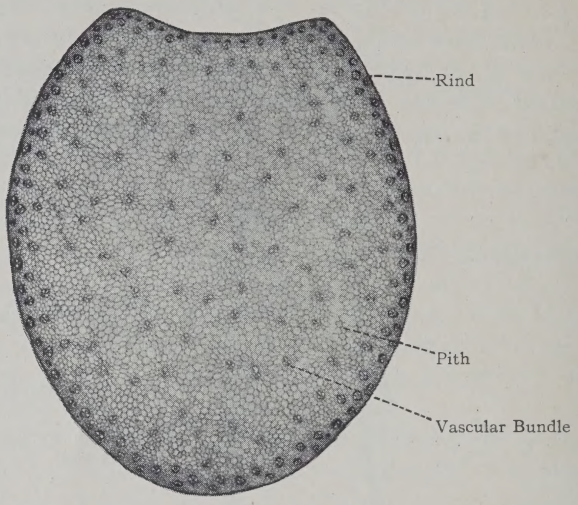


FIG. 81.—Cross section of a young internode of stem of Indian Corn (*Zea mays*) somewhat magnified.

stalk shows clearly the hard, shell-like rind and a large pithy center in which are seen irregularly spaced the cut ends of the veins, *vascular bundles* (Fig. 81). The rind in the full grown stem is composed of thick-walled cells, *sclerenchyma cells*, which impart strength to the stem. In the sclerenchyma region are numerous vascular bundles, usually smaller than those in the pith. The bulk of the pith, *ground tissue*, is composed of large, and very thin-walled cells with many intercellular spaces. Such thin-walled cells are *parenchyma* cells. They account for the soft character of the pith. The veins, or vascular bundles, extend lengthwise from node to node. If one cuts through the rind and pulls the stalk in two, many of the vascular bundles will be drawn out of the pith, and they will then appear as slender flexible threads, as seen in Fig. 82. At the nodes many of the bundles branch, and the branches connect with branches of other bundles. The bundles in the leaves connect with bundles in the stem. It will thus be

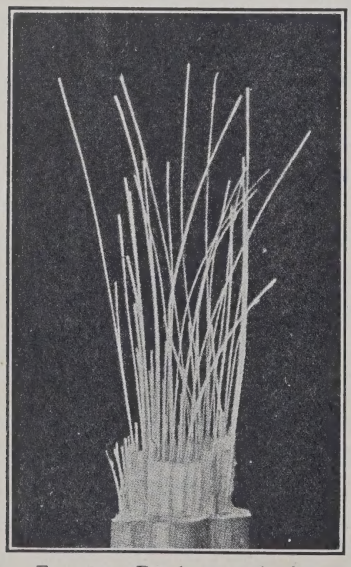


FIG. 82.—Broken end of corn stalk showing protruding vascular bundles. (After Atkinson.)

seen that the vascular bundles form one great system of tissue which transports water and food throughout the entire plant.

On examining the section in detail with the microscope, we find on the outside the epidermis, consisting of a row of small cells of uniform size. Beneath the epidermis is a zone of sclerenchyma cells in which are spaced the numerous smaller vascular bundles (Fig. 83).

This zone develops into the hard rind of the corn stalk. The soft pithy tissue composing the larger and central part of the stem consists of thin-walled parenchyma cells with intercellular spaces.

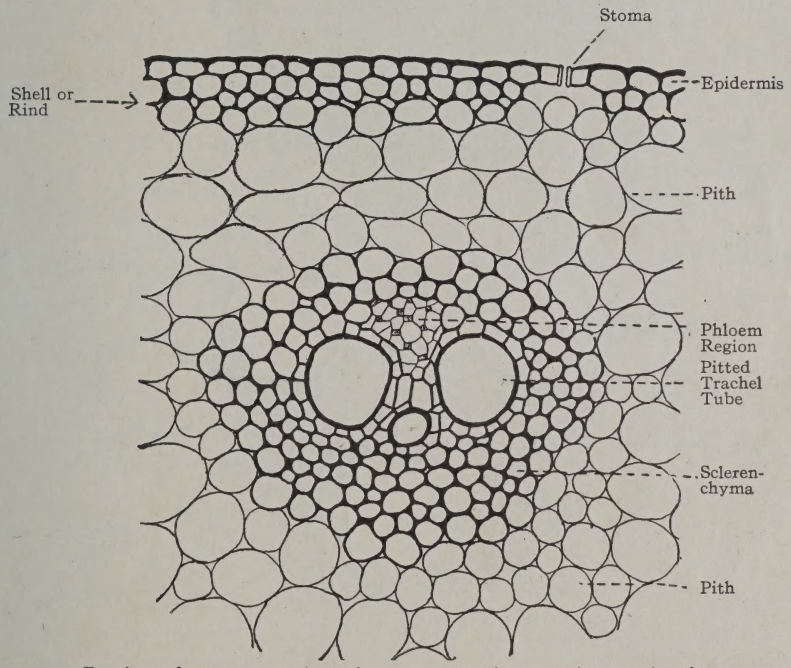


FIG. 83.—Portion of a cross section of outer part of young internode of corn stem.

The Vascular Bundle.—In the vascular bundle, the phloem and xylem lie side by side, the phloem facing the periphery of the stem (Fig. 84). At the outer edge of the phloem, is a narrow band of crushed cells, the *protophloem.* The rest of the phloem is composed of larger cells somewhat hexagonal in outline with small square cells distributed among them. The larger are the sieve-tubes, and the smaller, the companion cells.

In the *xylem* are generally present two large and conspicuous pitted tracheal tubes, or vessels. At the inner angle of the xylem region may be a large intercellular space. Bordering upon the intercellular space are two vessels, an annular and a spiral tracheal tube. These make up

the *protoxylem.* Surrounding the entire bundle, is a band of thick-walled cells, the *sclerenchyma sheath.*

The large intercellular space is formed by the breaking down of cells, while the intercellular spaces between the cells of the pith are produced by the separation of these cells at the corners.

A description of the tissue elements of the vascular bundle as seen in longitudinal section will be given in the discussion of the dicotylous stem.

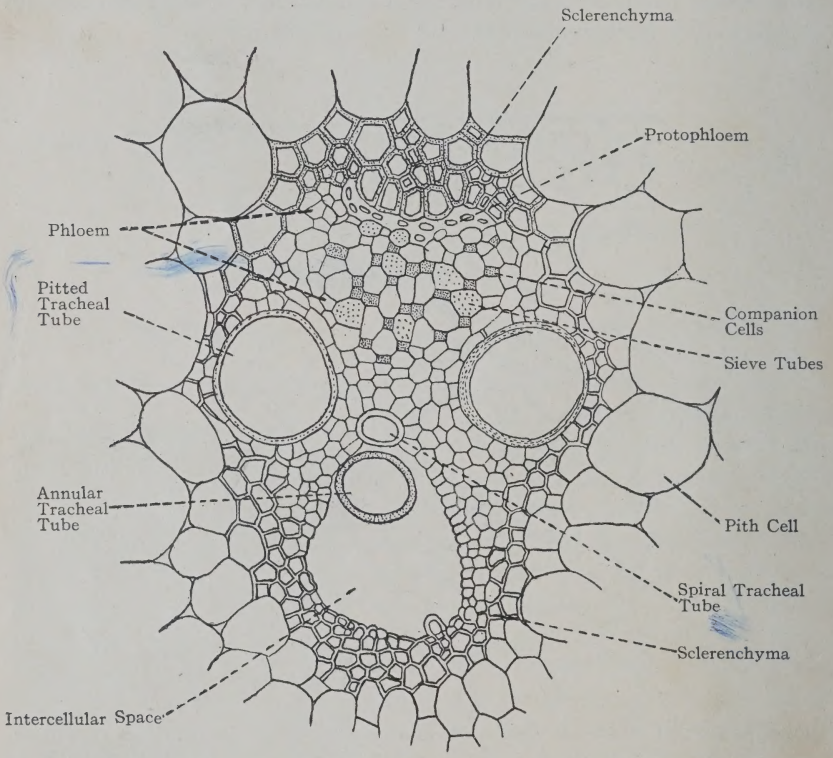


FIG. 84.—Cross section of a vascular bundle of an internode of the corn stem (*Zea mays*).

Stem of an Herbaceous Dicotylous Plant.—The stem of a typical dicotylous plant one year old or less is, in certain respects, more complex than that of the corn stalk. Here we find the vascular bundles forming a ring in the stem, which encloses a large central area of ground tissue, the pith, as shown in the photograph of a cross section of the wild sweet clover (Fig. 85). A diagram of the same cross section is shown in Fig. 86. Each vascular bundle is somewhat triangular in outline with the apex pointing towards the pith. These bundles run lengthwise in the stem

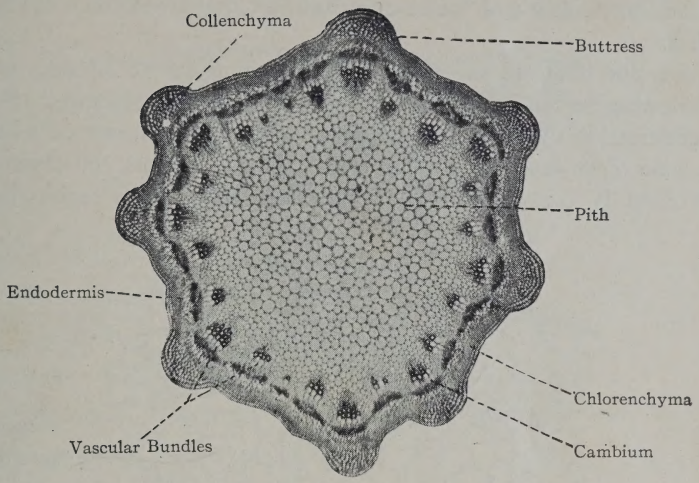


FIG. 85.—Photomicrograph of a cross section of a young stem of the white wild sweet clover (*Melilotus alba*).

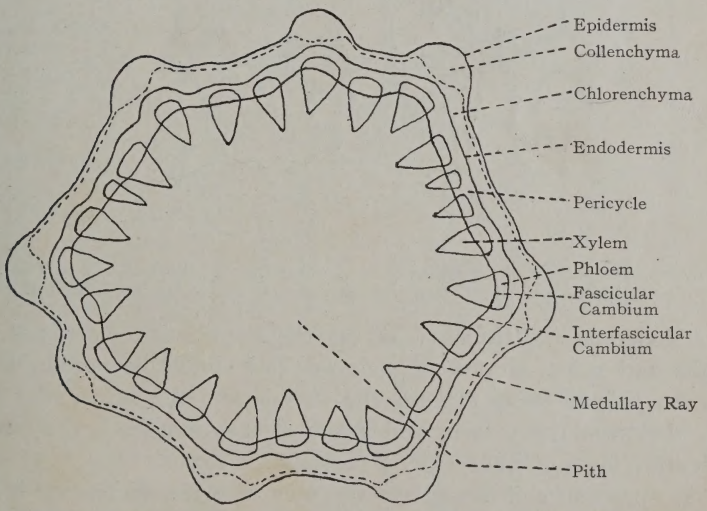


FIG. 86.—Diagram of a cross section of a young stem of the white, wild sweet clover (*Melilotus alba*).

at a uniform distance from the outside of the stem. They extend out into the leaves also, and because of that fact they are known as *leaf-trace* bundles.

Using the diagram as an aid and beginning at the outside, we note the following regions: the outer layer of cells is the epidermis. Beneath the epidermis is the cortex consisting of a layer of colorless cells followed by a zone of chlorophyll-bearing cells. The innermost cell layer of the green zone is the *endodermis*, or starch sheath. The region between

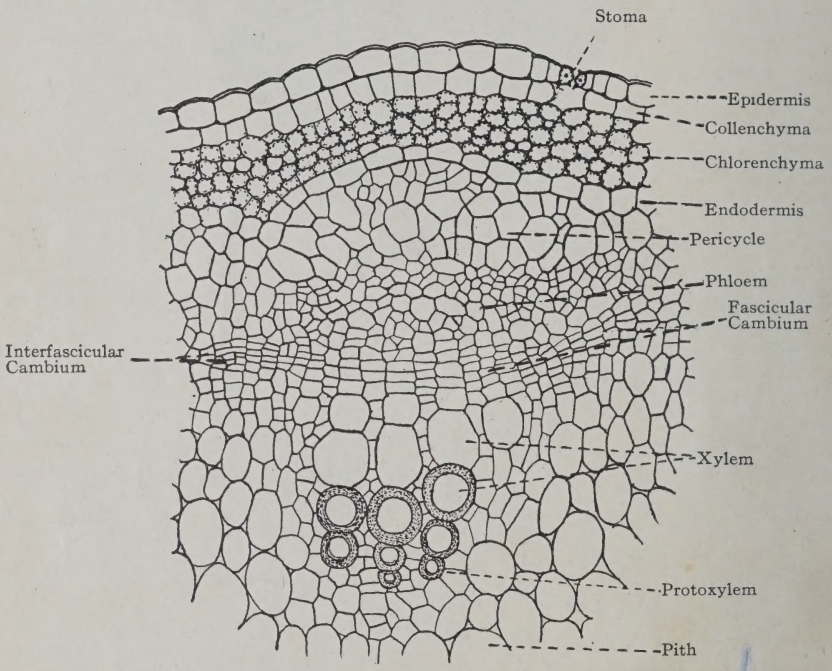


FIG. 87.—Cross section of a portion of the young stem of the white, wild sweet clover (Melilotus alba) including a small vascular bundle shown in detail.

the endodermis and the circle of vascular bundles is the *pericycle*. The phloem and xylem strands of each vascular bundle lie radially side by side, the phloem being towards the outside and the xylem next to the pith. Between the phloem and xylem of each bundle, is the *fascicular cambium*, a layer of embryonic, or meristematic cells.

The appearance of these tissues as seen with the microscope is shown in Fig. 87. Beginning at the outside, the epidermis appears as a row of rather uniform cells with outer and inner walls slightly thickened. Stomata are present. Beneath the epidermis is a row of similar cells which will mature as *collenchyma*. The external ridges or buttresses of this

stem are composed of collenchyma. A collenchyma, or thick-angled, cell is one whose walls thicken chiefly at the angles. Collenchyma tissue

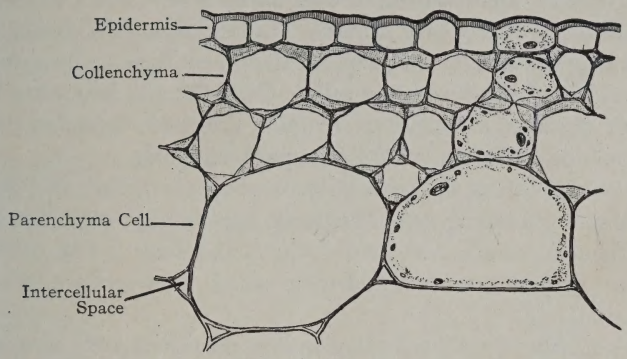


FIG. 88.—Cross section of cortex of stem, showing collenchyma cells beneath epidermis. (After Strasburger.)

combines strength with flexibility. Fig. 88 illustrates collenchyma cells more highly magnified.

Following the collenchyma is a band of parenchyma cells rich in chloroplasts, the *chlorenchyma*. In this region in many herbaceous stems,

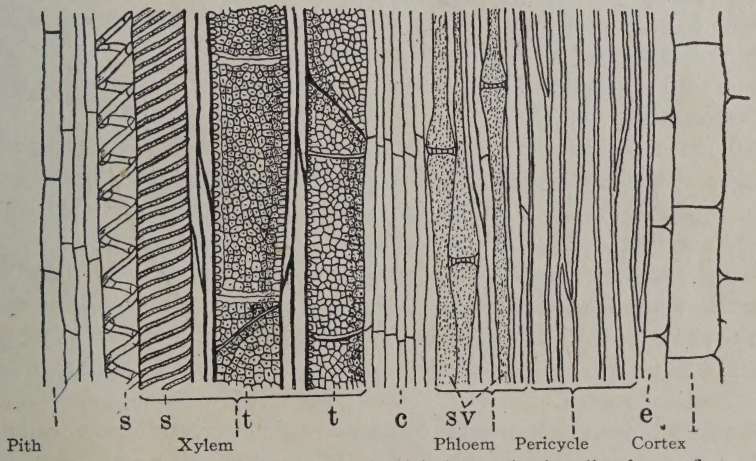


FIG. 89.—Longitudinal section of a simplified vascular bundle of a sunflower stem. *s*, *s*, spiral tracheal tubes or vessels; *t*, *t*, pitted tracheal tubes; *c*, cambium; *sv*, sieve-tubes; *e*, endodermis.

thick, stocky *sclerenchyma*, or "*stony*" cells, are present. These stony cells are short and thick-walled. They impart strength to the region in which they occur. In many plants mineral crystals are present in certain cells of the chlorenchyma. Within the chlorenchyma is the row of well defined

cells containing starch, the *endodermis*, or *starch sheath*. Beneath the endodermis is the region of the pericycle. Here it consists of relatively large thin-walled cells which will mature as bast fibers. The bast fibers are often more numerous radially opposite the bundles. Following the pericycle is the ring of vascular bundles. The phloem appears as a dense mass of relatively smaller thin-walled cells. Of these, the larger are the sieve-tubes, and the smaller cells next to them are the companion cells. The rest of the phloem constitutes the bast parenchyma.

The *fascicular* cambium between phloem and xylem, and the *interfascicular* cambium extending across between the bundles form a single layer of meristem, making a complete circle in the stem. The cells of the cambium are very thin walled, and their radial diameters are shorter than the tangential.

The xylem consists of tracheal tubes and parenchyma cells arranged in radial rows. The older elements of the xylem have thick walls. The smaller xylem elements, the first developed next to the pith, constitute the protoxylem. As the bundle ages some of the parenchyma cells may develop into wood fibers and tracheids. The walls of the tracheal tubes, wood fibers and tracheids of the xylem contain a characteristic substance, *lignin*, and such elements are said to be lignified. Thick-walled cells in other regions of the stem may contain lignin.

Phloroglucin and hydrochloric acid give lignified cells a rose color. They are stained a bright red with safranin.

The pith is composed of rather uniform thin-walled parenchyma cells with intercellular spaces.

A longitudinal aspect of the elements of a simplified vascular bundle together with those of the pericycle and a few cells of the pith and cortex, is illustrated in Fig. 89. At the left is the pith. Following to the right are the annular and spiral tracheal tubes (*ss*) of the protoxylem. The two large tracheal tubes (*t t*) are pitted. These may be surrounded by wood fibers and tracheids. The cambium is located at *c*. In the phloem are the sieve-tubes (*sv*) with their companion cells, and adjacent parenchyma. The fibers of the pericycle and the endodermis at *e* are followed by cells of the cortex.

Portions of a sieve-tube and companion cells in cross and longitudinal sections are shown in Fig. 90, A, B. The perforated cross wall is the sieve-plate (A).

It will be observed that the elements of mature primary tissues are greatly elongated.

As stated, Fig. 88 represents a simplified vascular bundle. The xylem of the bundle may contain the following elements: *tracheal tubes*, or vessels, *tracheids*, *wood fibers* and *wood parenchyma*. A tracheid is an

elongated, thick-walled cell with more or less tapering ends. The diameter of the cell is usually greater than the thickness of the wall (Fig. 91, B, C). There are spiral, annular, and pitted tracheids. An annular tracheid has its wall strengthened by ring-shaped thickenings on the inside. The spiral tracheid has spiral thickenings (Fig. 91, C). A pitted tracheid has a thick wall in which there are small rounded thin places or openings, the *pits* (Fig. 91, B). A fiber is a narrow, elongated, thick-walled cell with very tapering or sharp pointed ends. The diameter of the cell cavity is usually no greater than the thickness of the cell wall. Fibers add strength to the stem (Fig. 91, A). A tracheal tube, or vessel, is

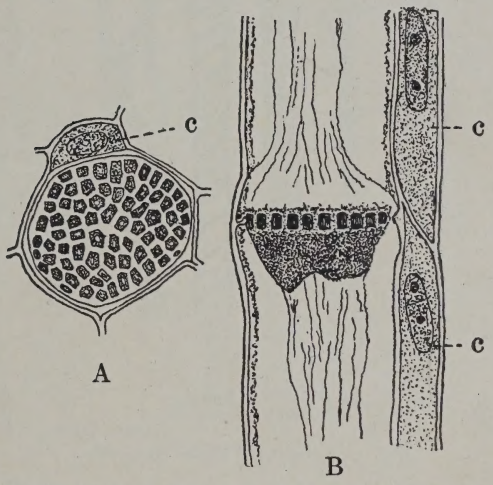


FIG. 90.—Sieve-tube of pumpkin stem. A, transverse sieve-plate seen from the surface. B, longitudinal section of portion of sieve-tube with a sieve-plate and portions of two companion cells; *c*, companion cell. (Strasburger, Macmillan Co.)

composed of a longitudinal row of two or more cells thrown into communication by the partial or complete absorption of the cross walls. There are annular, spiral, pitted, and reticulated vessels. The latter have reticulated or net-like thickenings (Fig. 92.)

Annular and spiral vessels occur in the protoxylem. They can be stretched and at the same time are kept open by the rings or spiral thickenings.

Pitted or reticulated vessels are formed chiefly after the stem has elongated.

The phloem is composed of sieve-tubes with their companion cells, bast fibers, and phloem parenchyma. A sieve-tube consists of one or more cells which communicate with each other or with neighboring cells through very fine openings aggregated in circumscribed areas, the sieve-

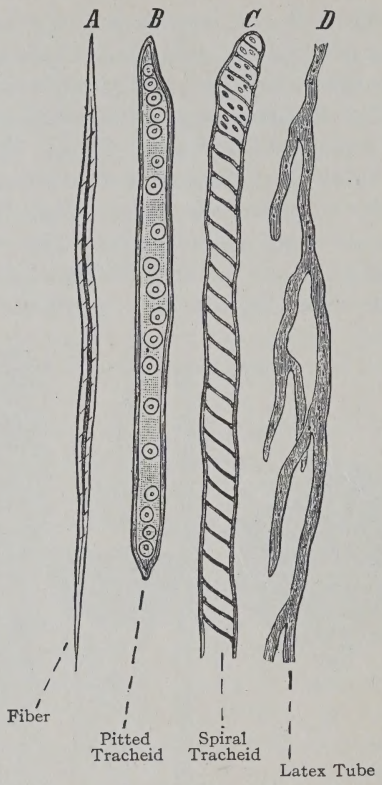


FIG. 91.—Isolated tissue elements.

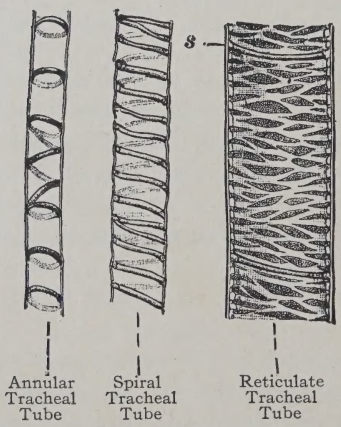


FIG. 92.—Annular, spiral, and reticulate tracheal tubes; *s*, remains of dissolved cross walls. (After Strasburger.)

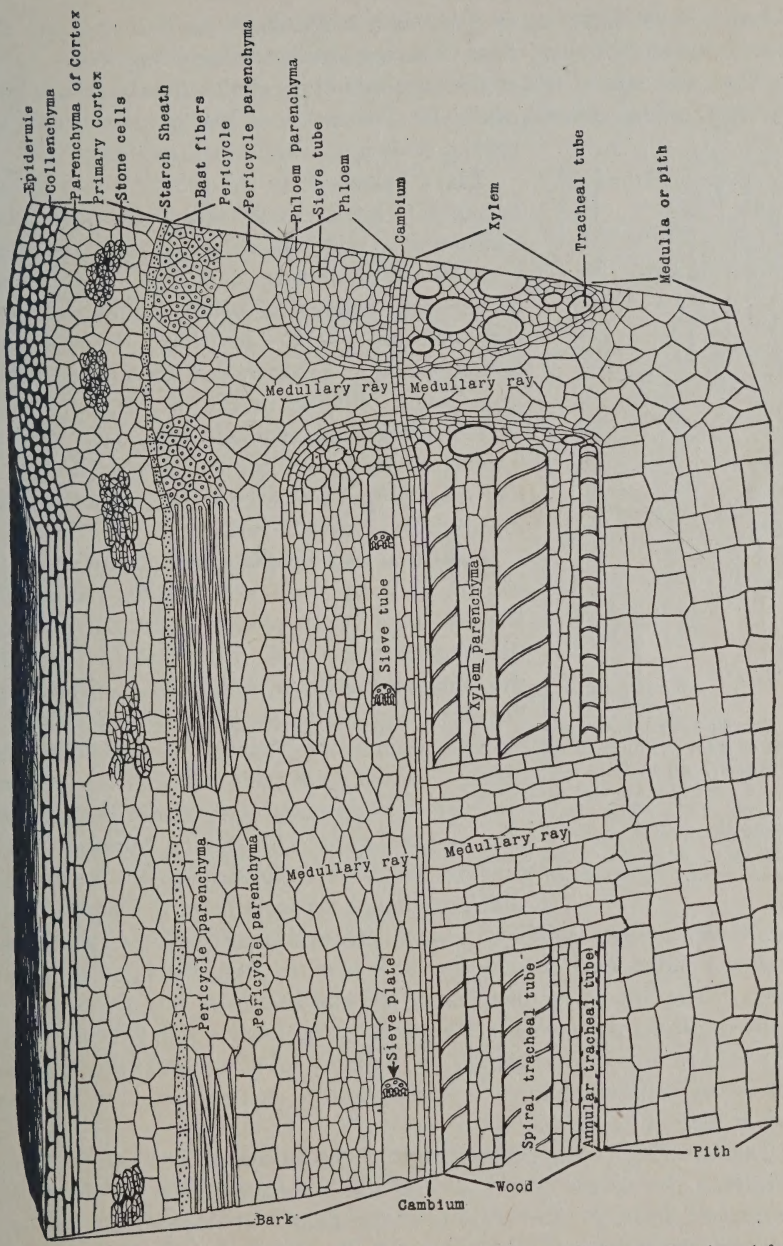


FIG. 93.—Diagram to show character and arrangement of tissues developed from primary meristem; cambial activity has not yet begun. (From Stevens' "Plant Anatomy.")

plates. Sieve-plates occur upon the longitudinal as well as upon the cross walls of the cells. Bast fibers are strengthening cells.

The structure of the stem composed of its adult primary tissues may be visualized in the diagrammatic illustration of Fig. 93, which shows a part of cross and longitudinal sections.

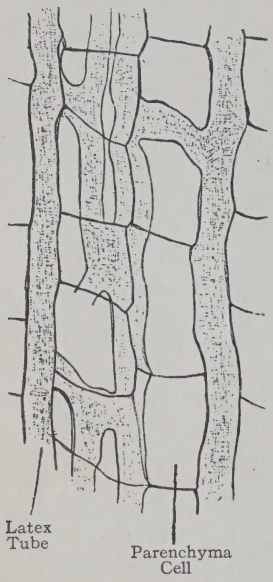


FIG. 94.—Tangential section of stem (*Scorzonera hispanica*), showing net-shaped latex tube among parenchyma cells. This form of milk tube is the result of a union of several cells. (Strasburger, Macmillan Co.)

Latex Vessels.—In the ground tissue of certain plants latex vessels occur which are tubes containing a milky fluid, *latex*, as in the common milkweed, lettuce, dandelion. Latex may be variously colored as in the Celandine Poppy (Stylophorum) and in the Bloodroot (Sanguinaria). Latex vessels are formed either from single cells, as in Fig. 91, D, or by the anastomosing of several cells (Fig. 94). It is of interest to note that the India rubber of commerce is derived from the latex of the so-called rubber-trees, Hevea, Ficus, etc.

Collateral and Bicollateral Bundles.—When phloem and xylem lie side by side, the bundle is collateral. When phloem is present both on the outside and on the side next to the pith, the bundle is known as bicollateral. Bicollateral bundles occur in the stem of the pumpkin.

The Course of Vascular Bundles in the Stem.—According to their course in the individual leafy stem, vascular bundles may be placed in two categories: (1) the cauline bundles, those that are confined exclusively to the stem, and that are formed acropetally as the stem grows; and (2) the common bundles, those which are common to both leaf and stem. Cauline bundles may or may not be connected with the bundles of the leaves. The bundle, or bundles, of the leaf that pass into the stem are known as *leaf trace bundles*. When followed from leaf into stem, they are found to pass down through two or more internodes and finally unite with other common bundles. Before uniting with other bundles they may or may not branch.

The Growing Point and the Origin of the Primary Tissues.—We may now trace the origin of the several tissues, discussed in the preceding paragraphs, from the growing end of the stem. The description of their origin will be more easily followed with the aid of diagrams of cross and longitudinal sections, as shown in Fig. 95.

The growing point of the stem is generally a conical or thimble-shaped mass of embryonic tissue, the *primordial meristem*. The cells are thin-walled, isometric, each possessing a relatively large nucleus and a dense cytoplasm with no visible vacuoles. They are always capable of growth

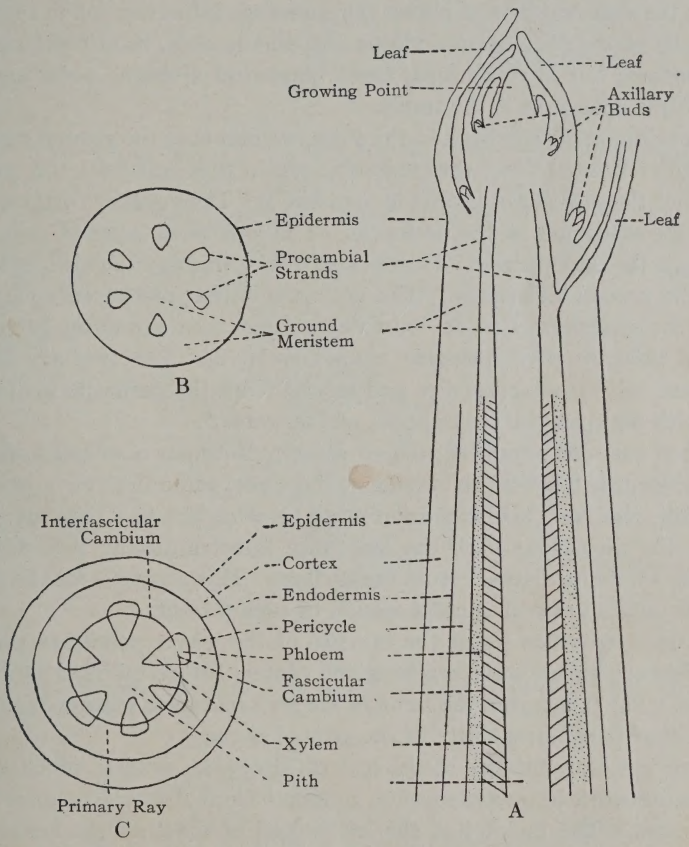


FIG. 95.—A, diagram of a longitudinal section of the distal end of a dicotylous stem. B, cross section a short distance back of growing point. C, cross section farther back as indicated.

and division. From the growing point primordia of leaves and axillary buds arise.

A short distance back of the growing point the primordial meristem is differentiated into three regions, the *protoderm*, which is the surface layer and which will give rise to the epidermis, the *ground meristem*, and the *procambial strands*, several in number. These three regions constitute the *primary meristem*.

The procambial strands are arranged in a circle, and each is completely surrounded by the ground meristem (Fig. 95, B). Each is composed of much elongated cells which are frequently pointed at the ends. In cross section these cells are smaller than those of the ground meristem. The procambial strands give rise to the vascular bundles.

In the vast majority of plants the epidermis is but one cell in thickness, the cells of the protoderm dividing anticlinally only, or at right angles to the surface; but in exceptional cases tangential divisions occur also, and a multiple epidermis is the result.

Continuing farther back in the stem, we find that the ground meristem has differentiated into the *primary cortex*, the *pericycle*, the *primary rays* and the *medulla* or *pith* (Fig. 95, A, C). The primary cortex extends from the epidermis to the pericycle. The innermost layer of cells of the cortex is the endodermis. It is located about midway between epidermis and the procambial tissue. The pericycle is the zone of cells extending from the endodermis to the vascular bundles and the outer extremities of the primary rays (primary medullary rays). The primary rays lie between the vascular bundles and extend from the pericycle to the pith. The pith occupies the central part of the stem.

Each vascular bundle consists of *phloem*, *fascicular cambium*, and *xylem*. The phloem is toward the outside of the stem, while the xylem is next to the pith, the fascicular cambium lying between the two (Fig. 95, A, C).

In the dicotylous stem the leaf trace bundles usually pass down the stem at a definite distance from the surface. This accounts for the regular ring of bundles seen in a cross section of such a stem.

In monocotylous stems the bundles of the leaves penetrate the stem to different depths, some reaching the center, before taking a downward course. For this reason the bundles are seen in a cross section of the stem to be distributed irregularly in the ground tissue.

The vascular bundles of the leaf of dicotylous plants, which usually form a network by anastomosing, generally unite into one or more larger leaf traces. The bundles of the leaves and of the stem are always connected from the start with the bundles of the roots, and, because of this fact, the vascular tissue of the whole plant forms a unified conducting system, the system of rapid transit.

Secondary Growth of the Stem.—In the young stem we find a ring of isolated vascular bundles, as stated in a preceding paragraph (Fig. 86). Such a stem consists wholly of primary tissues. During the growth of the first season in woody perennials and in many herbaceous plants which die at the close of the first season, a complete ring of wood and one of bast are established by the activity of the cambium. Tissues formed by the cambium are *secondary tissues*.

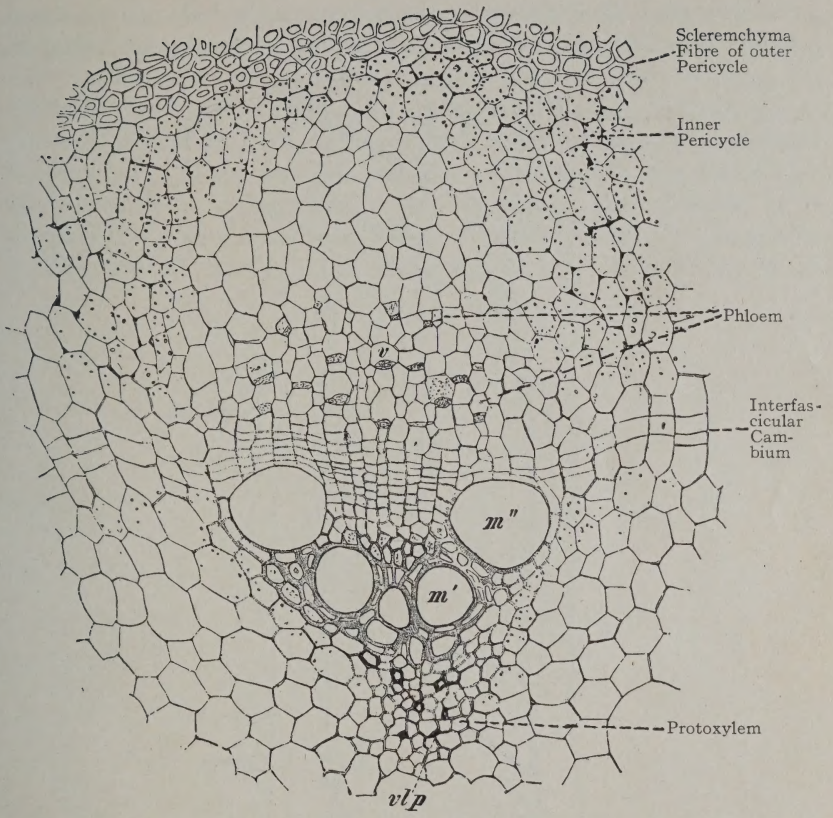


FIG. 96.—Cross section of vascular bundle and neighboring tissues of stem of *Aristolochia sipho* in the first year of its growth, showing cambium in active division. *m'*, *m''*, vessels with bordered pits; *v*, sieve-tube.

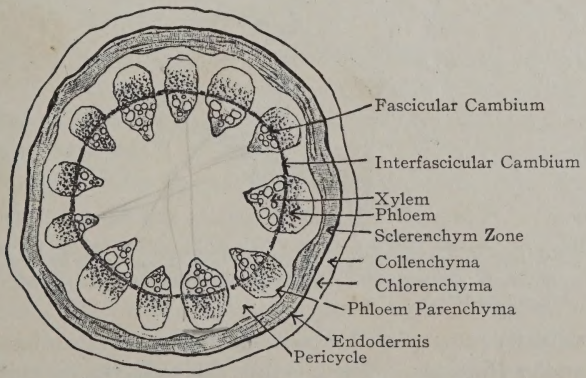


FIG. 97.—Diagram of a cross section of a stem of *Aristolochia sipho* 5 millimeters in thickness. Secondary thickening has begun. (Strasburger, Macmillan Co.)

Shortly after the beginning of the activity of the fascicular cambium, a row of *interfascicular cambium* cells is formed in the primary medullary

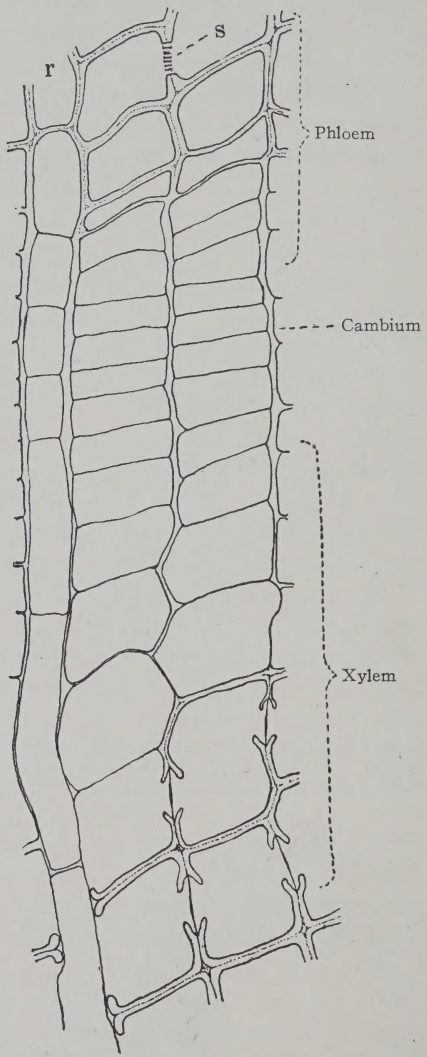


FIG. 98.—Portion of a cross section of the stem of *Pinus sylvestris*, showing young xylem cells and young phloem with cambium between; *s*, sieve area of sieve-tube. (Strasburger, Macmillan Co.)

rays, and which connects with the fascicular cambium of the adjacent vascular bundles (Fig. 96). There is thus established a continuous *ring of cambium* in the stem (Fig. 97). The wood and bast developed from the

interfascicular cambium connect with those regions of the vascular bundles, forming a complete *ring of wood* on the inner side of the cambium ring next to the pith, and a complete *ring of bast* on the outside of the cambium next to the pericycle. In plants which live but one year, growth proceeds no further. Frequently in such stems a zone of sclerenchyma fibers develops in the pericycle just beneath the endodermis, and a more extensive zone of collenchyma is formed beneath the epidermis, as in the pumpkin, clover, sunflower, Aristolochia, etc. (Fig. 97). In species of the crowfoot family (Ranunculaceae), such as those in the genus

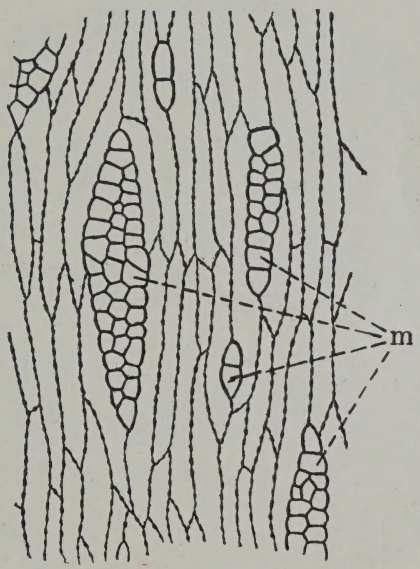


FIG. 99.—Tangential section through the cambium of the Elm, showing elongated form of cambium cells and end view of rays, *m*. (From F. O. Bower's "Botany of the Living Plant." By permission of the Macmillan and Company, Ltd., Publishers.)

Ranunculus, a group of sclerenchyma fibers is developed externally to the phloem of each bundle instead of a continuous zone encircling the stem.

The Origin of Phloem and Xylem from the Cambium.—As stated, the cambium consists of a single layer of meristematic cells. Each cambium initial divides tangentially into two cells. One (or both) of these subsequently divides in the same plane (Fig. 98). In this manner radial rows of cells result. The cells next to the phloem mature into secondary phloem on the inside of the old phloem, while those next to the xylem mature as secondary xylem on the outside of the old xylem. In like manner, cambium in the medullary rays adds new medullary ray cells to the rays in the phloem and new medullary ray cells to the rays in the xylem. A layer of one cell in thickness must persist as initial cambial

cells. The cells of the phloem may remain meristematic for some time dividing in various directions. It is evident that the stem increases in girth by radial divisions of living cells.

In a longitudinal radial section the cambium cells appear long and narrow with square ends (Fig. 89). If a longitudinal section be made in a tangential plane, the cambium cells will appear pointed and interlocked with one another (Fig. 99). The groups of cells at *m* in this figure are end views of young rays formed by the cambium.

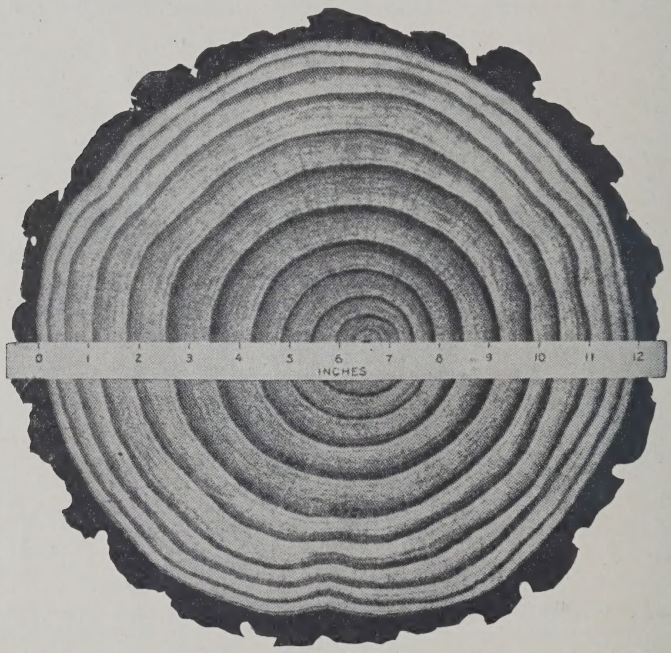


FIG. 100.—Cross section of a twelve year old tree trunk. The black, irregular outer zone is the bark. The darker bands indicate the summer wood of each annual ring and the lighter zones the spring wood. (From American Forests, Washington.)

Annual Rings.—In temperate regions a period of cambial activity during the growing season (spring and summer) alternates with a period of inactivity or dormancy extending through the winter months. Under normal conditions there is produced each year, by the ring of cambium, a layer or band of wood extending around in the stem. These bands are readily seen as concentric rings in a cross section of a branch two or more years old or on the end of a log (Fig. 100). They are known as *annual rings* of wood, owing to the fact that a ring is normally produced each year. An annual ring consists of two parts which are often readily distinguishable. The inner of the two parts is the *spring wood* and the

outer is the *summer wood*. The cells of the spring wood are larger and have thinner walls than those of the summer wood. The larger cells give to the spring wood the appearance of being very porous, while the summer wood appears more compact. The summer wood of one year adjoins the spring wood of the following year. The small, thick-walled elements of the summer wood of one year are adjacent to the larger thin-walled cells of the spring wood of the following year, consequently the line of demarcation is very sharp and frequently visible to the unaided eye (Fig. 100).

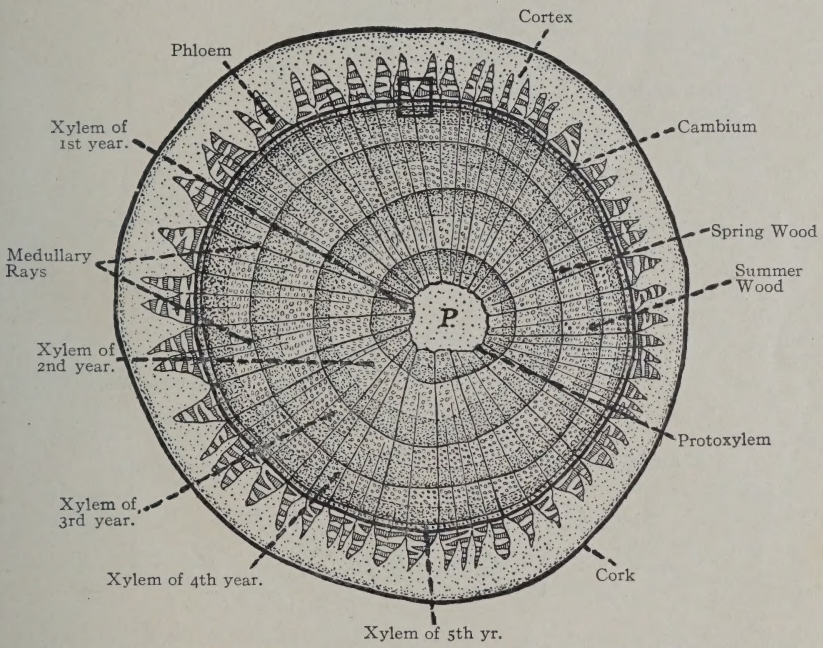


FIG. 101.—Diagram of a cross section of a stem of the Linden (Tilia), cut in the spring of the fifth year. (From F. O. Bowers' "Plants and Man." By permission of the Macmillan and Company, Publishers.)

If the normal rate of growth should be temporarily interrupted early in the season, owing to defoliation by insects or because of drought, two narrow rings of wood may be formed during spring and summer.

The Stem of the Linden.—The facts set forth in the preceding paragraphs on the secondary growth of the stem are well illustrated by a three or four-year old stem. Fig. 101 is a diagram of a cross section of such a stem. Three well defined regions are readily recognized: the central pith, the wood, and the bark. Between wood and bark is the cambium. The wood is disposed in well defined concentric annual rings, each ring representing usually a year's growth.

The lines running radially through the xylem are the *vascular rays*. Those that extend from the pith quite into the bark are the *primary rays*, while those that do not extend to the pith are the *secondary rays*. The

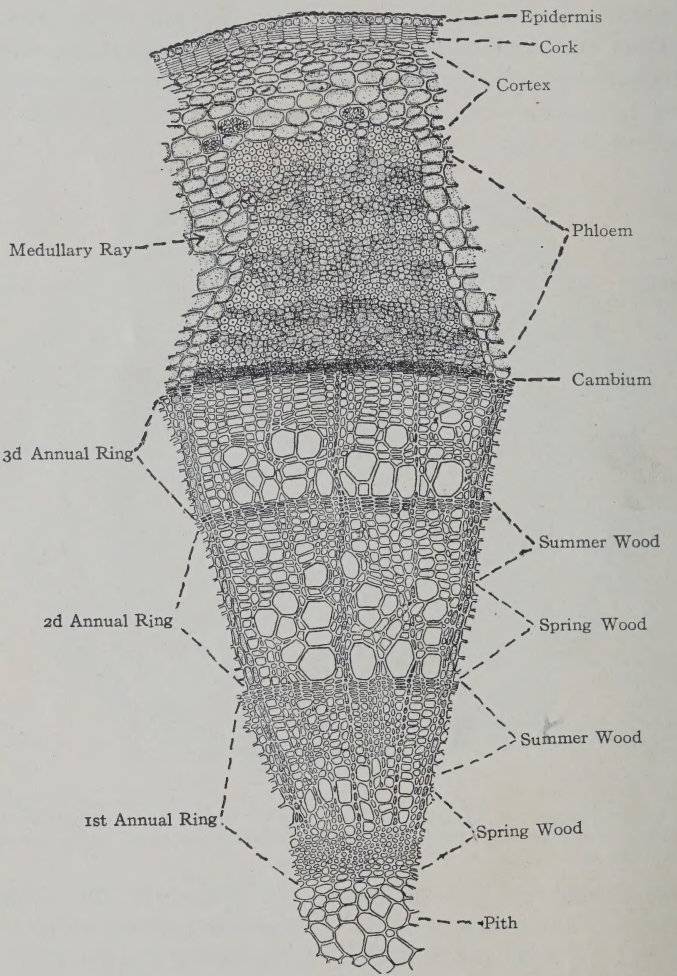


FIG. 102.—Microscopic view of a sector of the cross section of a three year old Linden stem, (*Tilia*). The phloem and xylem were derived from one vascular bundle. (Courtesy of Standard Scientific Corp., formerly Scientific Equipment Dept. of Kny-Scheerer Corp.)

greater the diameter of the stem, the larger is the number of the secondary rays formed by the cambium. The primary rays are usually two cells wide in a transverse direction, occasionally wider; the secondary rays are

one cell wide. In a vertical direction—up and down the stem —the rays may be several cells in height.

A strip of a cross section extending from pith to epidermis, as seen with the microscope, is shown in Fig. 102. The wood and bast of the strip represent a three-year old vascular bundle. The sharp line of demarcation of the annual rings is now quite obvious. In each ring the spring wood is composed chiefly of large pitted tracheae (tracheal tubes) while the summer wood is made up of relatively small cells consisting largely of wood

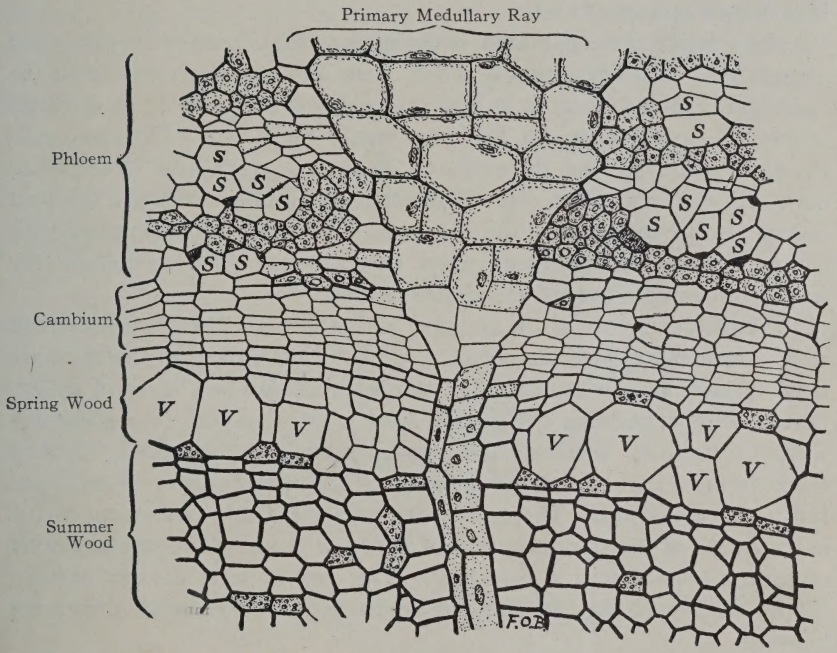


FIG. 103.—Stem of Linden. Detailed structure of the small square outlined in Fig. 101 magnified about 200 times. S, sieve-tubes; the dark spaces at one corner of the sieve-tubes are the companion cells. V, pitted tracheae. The summer wood consists of wood fibers interspersed with parenchyma. (From F. O. Bowers' "Plants and Man" By permission of the Macmillan Company, Publishers.)

fibers. The line of smallest cells constitutes the outer limit of each annual ring, and they present a sharp contrast with the large vessels of the spring wood of the following year.

In detail the xylem consists of large pitted tracheae, pitted tracheids, wood fibers, and wood parenchyma. The vessels, tracheids and fibers are devoid of protoplasmic contents. The wood parenchyma may contain living substance and stored food, such as starch and other substances. The tracheae conduct sap and dissolved substances. The wood fibers impart greater mechanical stability to the wood.

The masses of bast are somewhat keel-shaped, being narrower toward the outside (Fig. 101). These masses reveal alternating bright and dark layers running tangentially. The light, or shiny, layers are composed of very thick-walled bast fibers. The dark layers are composed of smaller cells (the bast parenchyma) containing starch, and larger cells (the sieve-tubes) with their companion cells. The number of bands of bast fibers is about twice that of the annual rings. It is readily seen also that the primary rays widen out funnel-wise at their outer ends, separating two keel-shaped masses of bast.

The activity of the cambium is the same as that described in preceding paragraphs. The formation of wood, bast, and medullary ray from the cambium is shown in detail in Fig. 103, which is that portion of the stem within the small square in Fig. 101, highly magnified. The large cells (S) of the bast are the sieve-tubes. Near each sieve-tube is the small dark cell, the companion cell. The small thick-walled cells are the bast fibers. In the spring wood the large cells (V) are the tracheae; those with contents indicated, represent wood parenchyma. The medullary ray widens out rapidly toward the chlorenchyma.

The chlorenchyma of the primary cortex forms a complete encircling zone. In many cells of the cortex, and of the outer parts of the rays, are large crystals of calcium oxalate. More externally is a layer of collenchyma cells, containing chlorophyll, and whose cell walls are glistening white in unstained sections, and especially thick at the angles. Finally the outermost part of the bark consists of the primary layer of cork, and lastly the epidermis. The epidermal cells are dead, and owing to the enlargement of the stem, are broken here and there. The primary layer of cork is several cells in thickness. The cork imparts the darker color to the surface of the stem and conceals the green color of the cortex beneath.

The bark consists of all the tissue from and including the epidermis to the cambium.

Formation of Cork.—Another kind of secondary tissue, the *cork*, is developed in the stem and roots of woody plants by the activity of a meristematic layer of cells known as the *cork cambium* or *phellogen*. Corky tissue is characterized by the presence in the cell walls of the remarkable water-proofing substance, the *suberin* or cork. The cork cambium arises usually just beneath the epidermis or a few cells deeper. By tangential divisions a layer of cells is produced. Those on the outside mature as cork, and constitute the *periderm* (Fig. 104). The inner cells produced by the cork cambium, the *phelloderm*, may contribute to the cortex and consequently increase its thickness. Cork is water-proofing material. This property is due to a substance, suberin, deposited in the

walls. A demonstration of this property may be seen in the tuber of the white or Irish potato. Potatoes unpeeled will remain fresh for days and even months in a moderately dry atmosphere. The rapidity, however, with which a peeled potato will dry out and become hard is a familiar phenomenon. Peeling "new" potatoes consists in removing the thin "skin" which is composed of the epidermis and the layer of cork beneath.

The protecting character of cork is indicated by its physical properties. Besides being impervious to water, it is a poor conductor of heat and electricity; it is not readily corroded by acids and alkalies; it does not

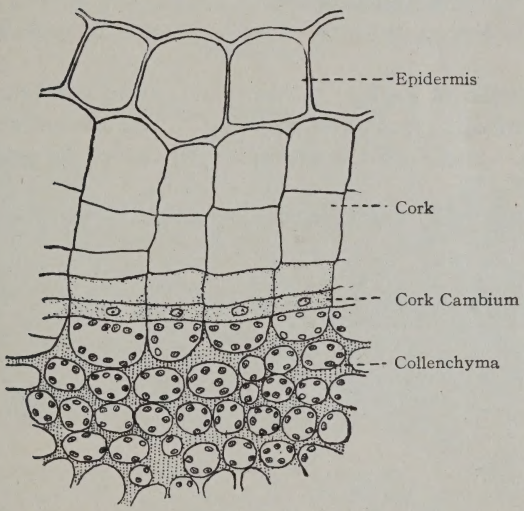


FIG. 104.—Cross section of cortex of stem of elder (*Sambucus canadensis*), showing cork and cork cambium. (Strasburger, Macmillan Co.)

decay rapidly, and it is not so likely to be eaten by insects and small animals as are many other parts of the plant.

Cell walls containing suberin turn yellow under a proper application of chlor zinc iodine, or sulphuric acid and iodine. In plants whose branches remain green, the epidermis lives longer, and the corky layer is slow in developing, or does not develop at all, as in the mistletoe, species of holly, Acacia, rose, and maple. Scattered over the surface of the stem are many small pustule-like protuberances, the *lenticels*.

Lenticels.—Lenticels are openings in the cork layer, which form a communication between the air and the live cells beneath. In other words they are ventilators in the cork. They are formed as follows: beneath certain stomata the cork cambium, instead of producing a layer of cork, will give rise to a mass of thin-walled cells with intercellular spaces;

by an increase in size these masses finally break through the epidermis and project beyond the surface of the stem (Fig. 105).

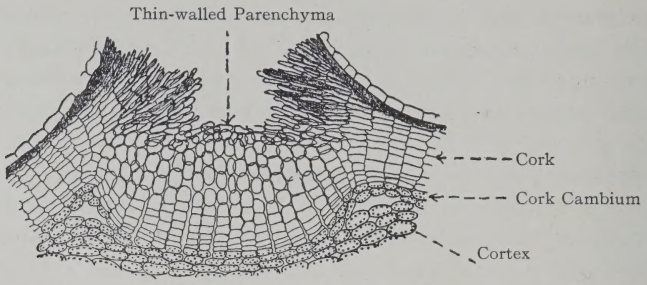


FIG. 105.—A lenticel of the elder (*Sambucus nigra*) seen in section. (From Haberlandt.)

The Formation of Bark.—As dicotylous stems and branches age the outer bark gradually cracks and scales off. The manner of cracking and scaling usually varies with the species. All tissues external to the cork

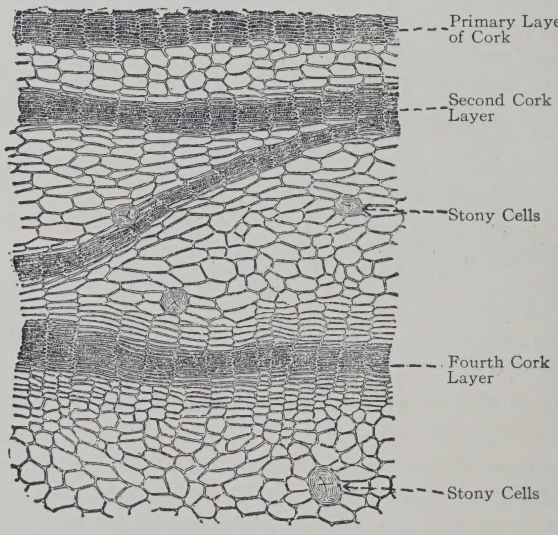


FIG. 106.—Cross section of a part of the bark of Cinchona, showing successive layers of cork with thin-walled cells between in which are a few stony cells. The layers of cork are lines of weakness along which flakes or strips of bark split off. (After Warnecke.)

cambium, being cut off from supplies of water and food, die. The first layer of cork cambium, except in such trees as the beech, soon ceases to be active. Another layer of cork cambium forms deeper in the stem and its activity soon comes to an end. Another layer forms still more deeply, as shown in Fig. 106, and its activity ceases also. This process

continues until layers of cork are formed ultimately in the living tissue of the secondary bast. Consequently in very old stems all the remaining tissue external to the cambium is of secondary origin.

Although the cambium forms a new layer of bast each year, the bark of the oldest trees is relatively thin because of the fact that the outer layers split off and fall away in strips or flakes in a manner characteristic of the species.

In the majority of our forest trees the layers of cork beneath the primary layer do not form even continuous zones parallel with the surface, but they are spoon-shaped (arcs of the circumference), and represent an undulating or festoon-like succession of inward curves. The inward curves of the succeeding spoon-shaped layers alternate somewhat with the inward

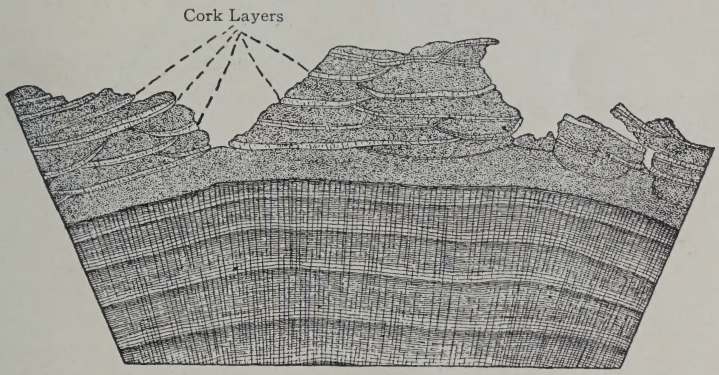


FIG. 107.—Cross section through bark and wood of an old Elm tree trunk, showing layers of cork and abscission of bark. (From Ganong's "Textbook of Botany," Macmillan Co.)

curves of those of the layers preceding, the result appearing in cross section as shown in Fig. 107. In all such plants the bark will break off in strips or flakes, *scaly bark*. The layers of cork constitute softer tissue, and they represent lines along which the scales of bark separate.

If, on the contrary, the corky layers form complete concentric rings, hollow cylinders of tissue become the *ringed bark*, such as is found in the grape vine, cherry, clematis, and honeysuckle. In the birch and cork oak, the periderm, which may become rather thick, is composed of alternating dense and loose layers which are responsible for the peeling off of the thin sheets of bark. The white color of the birch bark is due to "birch resin" (betulin) present in the cells.

Healing of Wounds.—Wounded or injured parts of land plants manifest various phenomena in response to such injuries. In the simpler cases the injured cells die, dry out, and become brown, while the uninjured cells

beneath may develop corky walls. In the case of large wounds in the seed-bearing plants, a cork cambium develops below these injured cells forming wound cork. In stems of woody plants, wounds which extend into the wood become surrounded and finally covered over by an outgrowth of tissue termed *callus* which arises from the exposed cambium. While the callus tissue is in process of gradually covering the wounded surface, an outer covering of cork is formed, and simultaneously a new layer of cambium is developed within the callus from a layer of cells continuous with the cambium of the stem. When the margins of the overgrowing

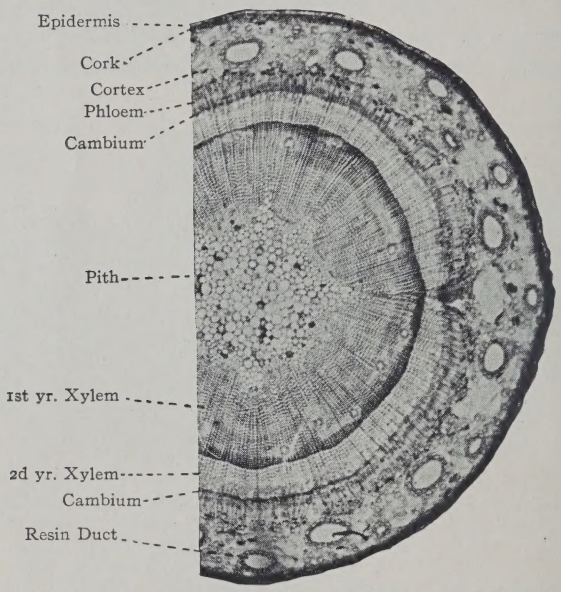


FIG. 108.—Portion of cross section of pine stem, showing first annual ring of wood and the spring wood of the second year.

callus tissue meet and close over the wound, the edges of its cambium unite to form a complete cambial layer of the stem over the wound. In this manner the wood exposed when a branch is sawed off may in a short time be completely covered over, leaving no external trace of the former injury. The callus wood never coalesces with the old dead wood. The wound is merely "heeled" over. In trees like the cherry the wounded cambium produces a mass of parenchyma cells which undergo gummosis.

The Pine Stem.—In the pine seedling the primary tissues are similar in arrangement and structure to those of an herbaceous stem of a dicotyledonous plant. In a two-year old stem, for example, we find in the center the pith which is primary ground tissue (Fig. 108). Surrounding this are two concentric rings of xylem, the annual rings, each the result of one

season, or one year's activity of the cambium. The fine radiating lines are the rays. The primary rays extend quite to the pith; those that do not reach the pith are secondary rays. Continuing outwards beyond the cambium is the zone of phloem and following this is the primary cortex in which are resin ducts. Resin ducts are tube-like cavities containing resin. They are surrounded by thin-walled living cells which secret resin. Many cells of the cortex contain chloroplasts.

The surface layer is the epidermis, the cells of which are now dead. Beneath the epidermis is the layer of cork.

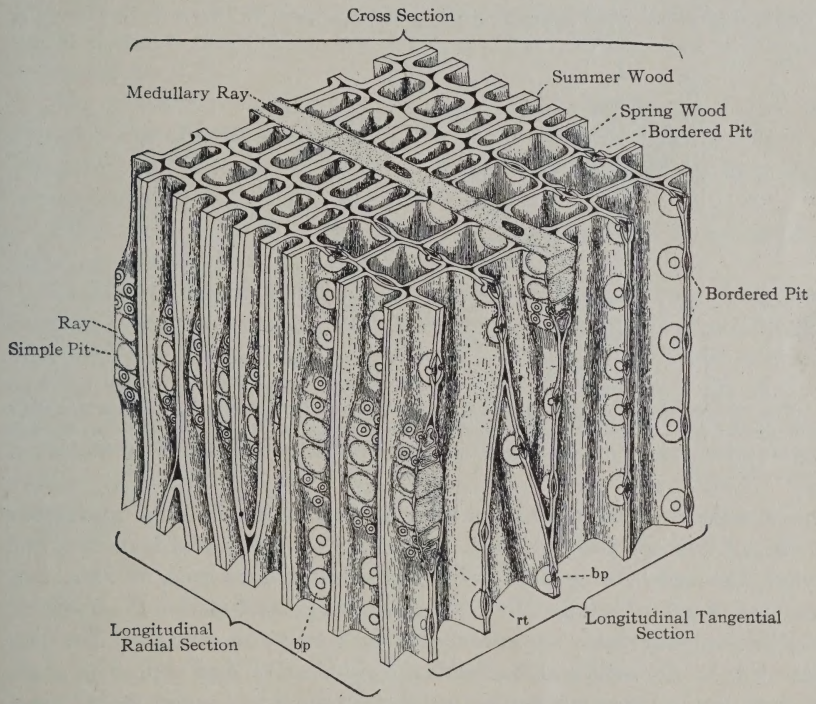


FIG. 109.—Perspective of a bit of pine wood including spring and summer wood; *rt*, ray tracheid; *bp*, bordered pit.

The Mature Xylem of Pinus.—The bulk of pine wood consists of thick-walled cells arranged in radial rows. As will be seen from longitudinal sections, these cells are pitted tracheids and wood fibers, tracheal vessels being absent. Those tracheids formed during the earlier part of the period of growth are larger than those formed later. The large cells of the spring wood (Fig. 109), following abruptly the smaller elements of the latter part of the preceding season, present a sharp line of demarcation. Consequently, each year's increment of xylem appears as a well defined ring.

The radial walls of the spring wood especially are marked by characteristic *bordered pits* (*bp*), appearing in cross section as two V's with the divergent limbs turned toward each other. Each bordered pit is a thin place in the cell wall, circular in outline, and with an overarching edge. In longitudinal radial views of the tracheid, the bordered pits appear as concentric circles. The inner circle represents the opening into the cell cavity, the outer circle being the outer limit of the pit next to the middle lamella. The thin partition with its centrally thickened part, the *torus*, is the primary layer of the cell wall, or closing membrane (Fig. 110). The closing membrane permits liquids to pass from cell to cell, but inhibits

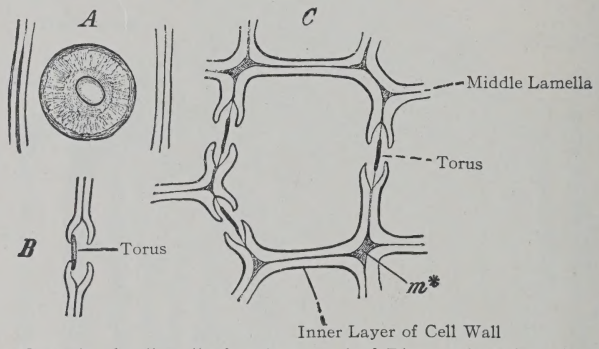


FIG. 110.—Details of cell wall of spring wood of *Pinus sylvestris*. *A*, surface view of bordered pit. *B*, longitudinal tangential section of bordered pit. *C*, cross section of entire tracheid; *m**, thickening of middle lamella at corners of cells. (Strasburger, Macmillan Co.)

the passage of bubbles of air, which tend to interfere with the movement of water through the tracheids. In a longitudinal radial section of the xylem the cells are seen to be elongated tracheids with interlocking, rounded or pointed ends. In longitudinal tangential section the bordered pits present the same appearance as in transverse section. The pits between the ray cells and tracheids are simple pits, and appear as single circles. In a tangential longitudinal section the rays are seen in end view.

The rays are thin strips of cells running in a radial direction. They are usually one cell in width but may be many cells in height, i.e., up and down in the stem. The upper and lower edges are flanked by pitted tracheids (*rt*). Resin ducts extend up and down in the wood. Those in the rays connect with the vertical ducts.

Heartwood and Sapwood.—In very young trees all the wood is sapwood. It is saturated with water and many of the cells contain living substance. In older tree trunks as in the red mulberry, black locust, red cedar, etc., we see that the woody cylinder consists of a darker central region, the *heartwood*, surrounded by the lighter colored zone of *sapwood*.

The outer layers of sapwood remain saturated with water, and it is through the sapwood that water ascends in the tree trunk.

Sapwood is changed into heartwood by the deposition in the cell walls and cell cavities of various substances such as resins, gums, tannin, mineral elements, and pigments. These substances give to the heartwood its color and durability, and at the same time render it unfit as water conducting tissue. The vessels of the older wood in many trees are plugged by parenchyma cells, *tyloses*, which develop from growths of adjacent wood parenchyma cells, and which penetrate the thin places in the walls of those vessels. Tyloses are present in the wood of such trees as the black locust (*Robinia pseudacacia*), the white oak (*Quercus alba*) and in the stem of the pumpkin, &c.

The pigments impart the characteristic colors to the various woods. Woods which are durable in contact with the soil owe their durability to the substances mentioned above. Those substances prevent in a large measure the growth of the wood destroying fungi.

Black locust and white oak wood have been found to be sound after standing longer than forty years as fence posts.

The Development of Tall Smooth Trunks, or Boles, Which Yield Clear Lumber.—In thick stands of native or cultivated forests, the trees become very tall early in life. As a result of the lack of light, the lower branches die and fall away when relatively small, and the result is a tall smooth trunk. The layers of wood added after the disappearance of the branches are uniform in character and free from knots. Such trunks yield clear lumber of the finest quality. A knot is a section of a branch. The remains of limbs which have dropped off appear as "dry knots" in sawed lumber. If the branch remain alive on the tree, the secondary wood will grow around it, and a "live knot" is the result.

After the tree is three or more years old, we see that the bulk of the trunk is composed of wood, while the bark is relatively thin. This is due chiefly to the fact that the cambium adds cells to the wood much more rapidly than to the bast. In some trees the pith hardens with age, while in others it may disappear, leaving cavities. The supply of lumber produced each year is due to the amount of wood added by the cambium. When growing conditions permit the addition of a ring of wood one inch wide per year, the forest produces approximately twice the quantity of lumber as when annual rings one-half inch thick are developed. Careful measurements in a given area of forest show us just how many board feet of lumber the area will yield per year.

Growth in Thickness of Monocotylous Stems.—Barring exceptions, cambium is not present in the vascular bundles of monocotylous plants. Consequently the vascular bundles do not increase in size with age. The

increase in diameter of the stem is brought about by the growth and division of the cells of the ground tissue in the embryonic region or regions. New vascular bundles are differentiated in the new ground tissue of the enlarged parts.

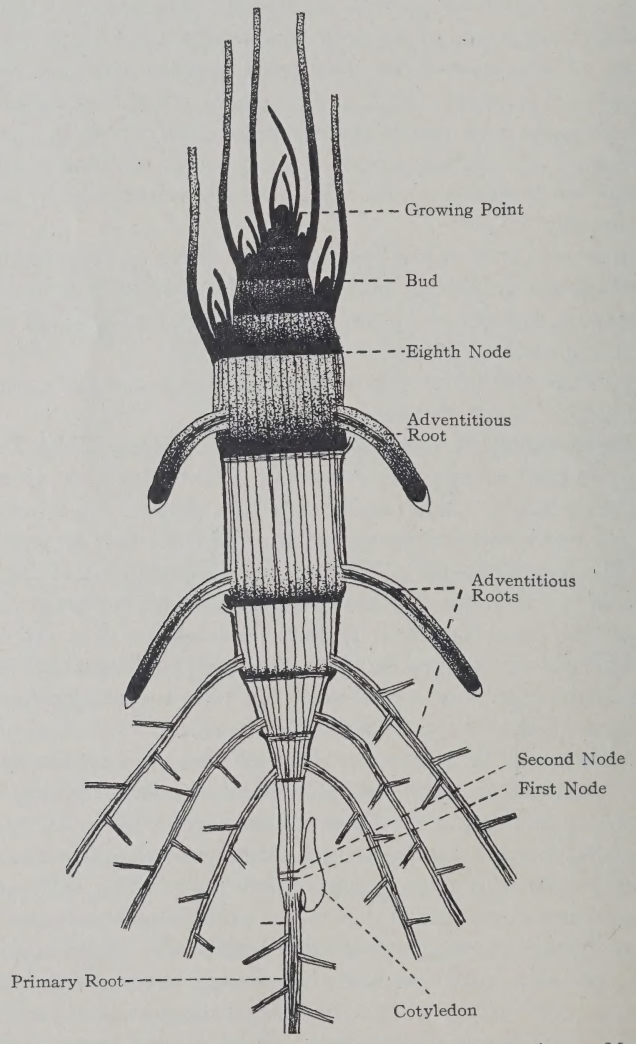


FIG. 111.—Diagram of a longitudinal section of a young corn plant. Meristematic regions are shaded black.

In our flora a few monocotylous plants increase in diameter by means of cambium. The Yucca is an example. The entire body of the adult monocotylous plant may be composed of mature primary tissues.

Increase in Diameter of the Corn Stem.—The stem of the seedling, consisting of a few nodes, scarcely exceeds three or four millimeters in diameter, while that of the thickest part of the mature stem may be as large as one's wrist (5 cm. or more).

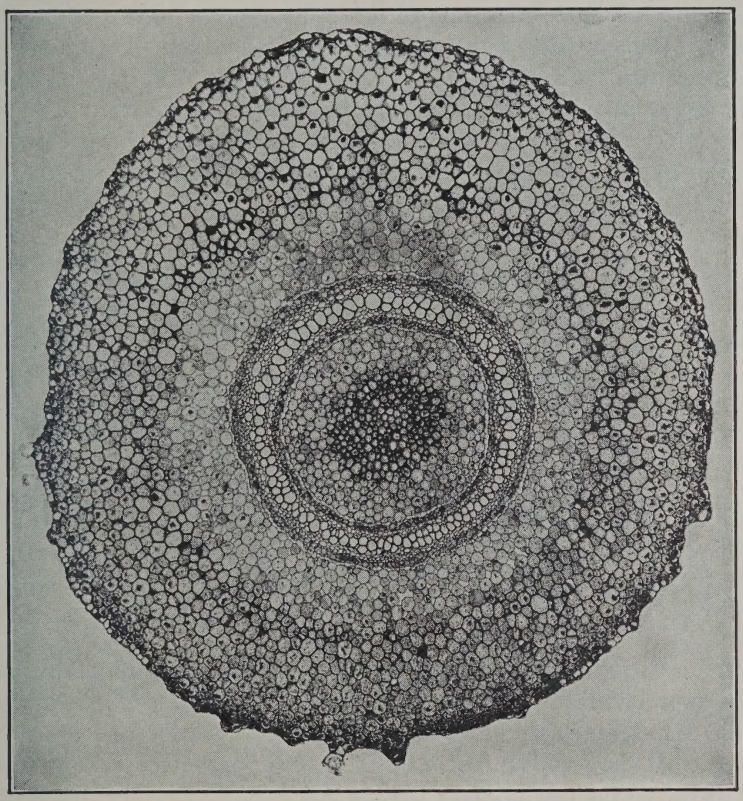


FIG. 112.—Cross section of the stem of *Dicksonia punctilobula*. Beginning at the outside the tissues are as follows: the epidermis, the cortex, and the vascular cylinder (siphonostele) enclosing the pith; in the vascular cylinder, the outer phloem, the xylem and the inner phloem; the endodermis which surrounds the cylinder on the outer and inner sides belongs to the ground tissue. (From Chamberlain's "Methods in Plant Histology.")

These first few nodes and internodes do not thicken appreciably with age, but those which develop subsequently become thicker until the maximum diameter is reached (Fig. 111). When any growing internode has attained its adult size it does not become any thicker with age. The increase in size results from the multiplication of ground tissue cells in the meristematic regions back of the primordial meristem. Meristematic

tissue persists for some time at the base of each internode, and it is from these regions that secondary roots develop.

As meristematic development ceases at the growing end of the stem with the formation of the tassel, the terminal internodes, those above the ear, elongate rapidly with but relatively little increase in thickness.

The Fern Stem.—The stem of our ordinary ferns (Polypodiaceae) is usually a branched rhizome growing horizontally upon the soil or a few inches beneath its surface. Leaves tend to spring from the upper side and roots from the lower. The growing point is not protected by scale leaves but by the young foliage leaves and numerous brown hairs and scales or only by the latter. The primordial meristem consists of a large apical cell from which the protoderm, the ground meristem and the

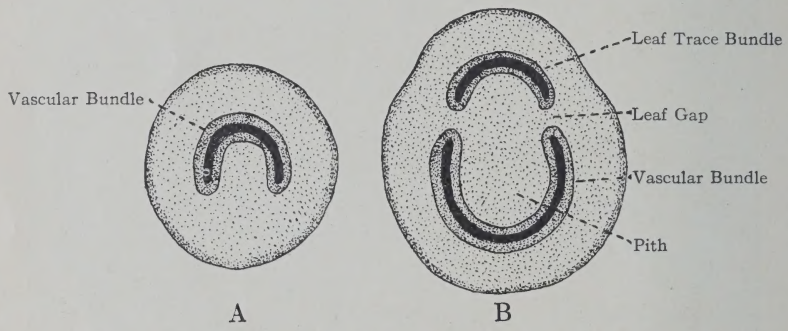


FIG. 113.—Diagrams of cross sections of leaf stalk A, and stem, B, of Adiantum Xylem black, phloem stippled.

procambial strand or strands are derived. There are no axillary buds. In the unbranched stems the apical cell is the continuation of that originating in the stem quadrant of the embryo. Secondary tissues are not developed in the fern, consequently the mature parts of the plant consist only of the permanent primary tissues.

In the mature stem of *Adiantum pedatum* or *Dicksonia punctilobula*, the type used as our illustration, the procambium arises as a cylindrical zone enclosing the pith. This zone differentiates into a central xylem completely surrounded by the phloem (Fig. 112). The endodermis forms a complete boundary between ground tissue and the vascular cylinder both externally and on the side next to the pith.

From the young procambial cylinder strands pass off into the leaves. Just above the insertion of each leaf-strand a small area does not differentiate into vascular tissue but consists of ground tissue, which connects the pith with the peripheral ground tissue. The vascular cylinder appears thus to be perforated by the ground tissue.

The space occupied by the connecting ground tissue is a *foliar gap*. The vascular tissue of the stem consists, therefore, of a perforated cylinder, a perforation, or foliar gap, being present at the insertion of each leaf trace.

If the section be made to pass through the stem at the base of a leaf, the vascular tissue will appear as two crescents with their openings facing each other, while in the leaf stalk a single crescent will be seen in the form

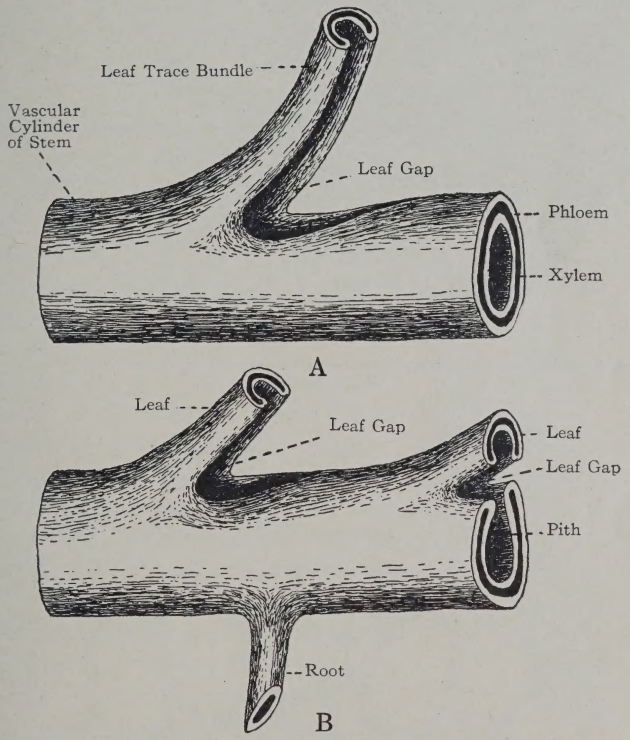


FIG. 114.—Perspectives of portions of the vascular system of Adiantum (cortex and pith omitted).

of a horse-shoe (Fig. 113, A, B). Fig. 114 which represents portions of the vascular cylinder only, the ground tissue being omitted, will greatly aid in visualizing the form of the vascular system.

A cross section of the stem just below the base of the leaf will show the ring-shaped zone of vascular tissue with enclosed pith, and surrounding peripheral ground tissue (Fig. 112).

In the type of stem illustrated by the brake fern (*Pteris aquilina*), separate procambial strands are formed in the adult stem just back of the growing point. The main strands, which are connected by short

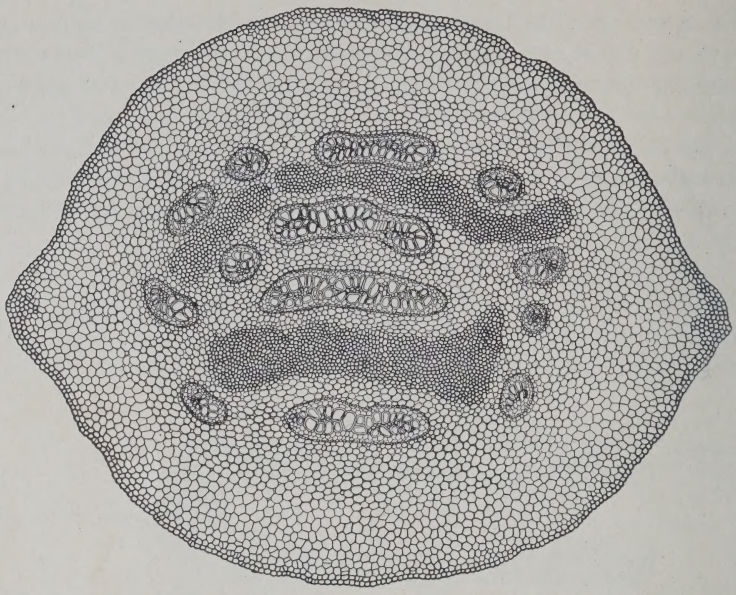


FIG. 115.—Cross section of the stem of the Bracken Fern (*Pteris aquilina*). Explanation in text.

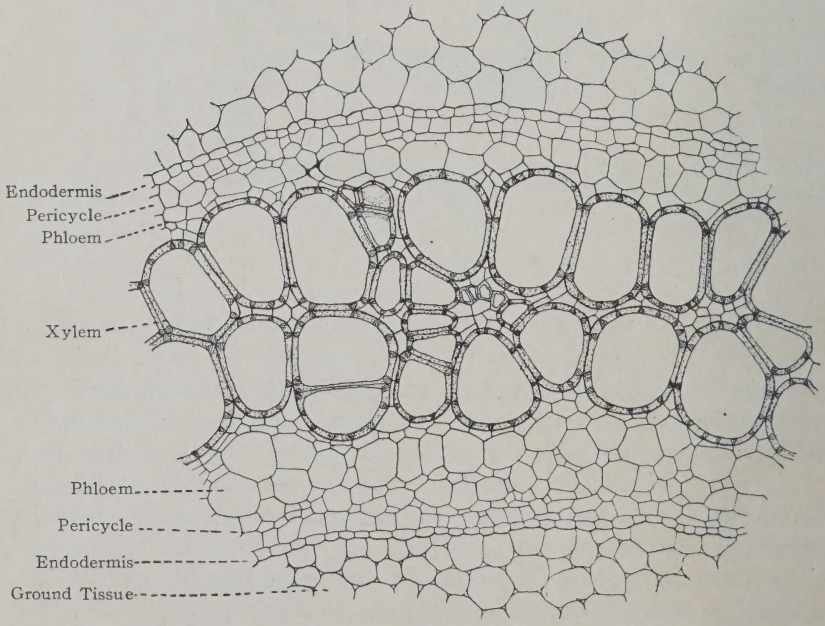


FIG. 116.—Cross section of portion of vascular bundle of *Pteris aquilina*.

branches, send off leaf traces to the leaves. The result is a vascular net work instead of a perforated cylinder. A cross section of the stem of Pteris is shown in Fig. 115, in which are seen the several vascular bundles.

The peripheral ground tissue of the fern stem consists largely of golden-brown thick-walled cells. Stony cells may occur also in the pith region. In the bracken stem two bands of stony tissue run lengthwise near the center of the stem, between which are the two main vascular strands (Fig. 115).

Turning our attention now to the detailed structure of the vascular tissue, we see, in cross section, that it is surrounded by a clearly defined row of cells, the *endodermis*, or *bundle sheath* (Fig. 116). The central part is composed of large, thick-walled cells, the *xylem* which is surrounded by the phloem. The phloem consists of thin-walled cells, many of the larger being sieve-tubes. One or two rows of cells just within the endodermis make up the *pericyle*.

The xylem appears as thick-walled cells closely pressed together. The conspicuous line separating the cells is the *middle lamella*. As will be seen in a longitudinal section, the xylem is made up largely of elongated tracheids with numerous transverse pits arranged like the rungs of a ladder (Fig. 117, A). For this reason these cells are called *scalariform tracheids*. The xylem first developed in the bundle (protoxylem) consists of smaller tracheids with spiral or reticulate thickenings. The longitudinal walls of the sieve-tubes are marked by numerous sieve areas (Fig. 117, B). Within the various parts of the ground tissue are often developed strands of dark brown sclerenchymatous cells (stony tissue), which give to the stem a certain rigidity. These cells have very thick, striated and pitted walls.

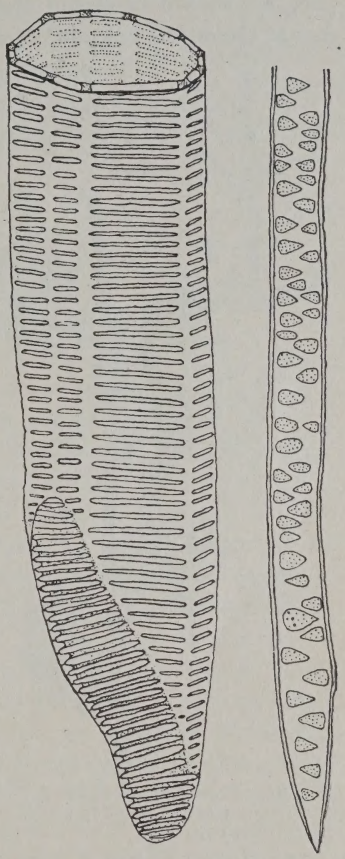


FIG. 117.—A, portion of a scalariform tracheid of Pteris. B, sieve-tube with numerous sieve-plates.

Modified Stems and Their Special Functions.—In presenting stem structure in the foregoing paragraphs, we have selected those which may be regarded as typical of the majority of plants. Differing from the

ordinary type, are very many which owe their differences to duration, habitat, and special functions.

As to duration, stems, as well as whole plants of which they are a part, are known as *annual*, *biennial*, and *perennial*. An annual is one that dies at the end of one year or growing season. An annual plant completes

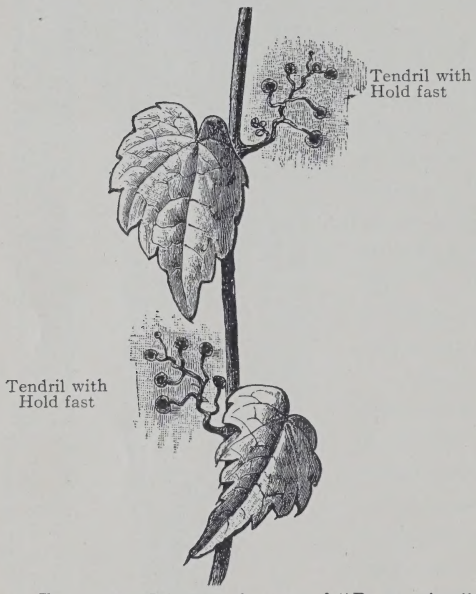


FIG. 118.—Piece of stem of "Boston ivy" (*Psedera veitchii*) clinging to a wall. (Strasburger, Macmillan Co.)

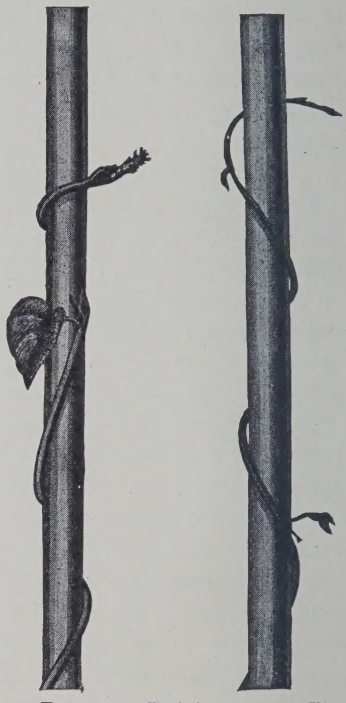


FIG. 119.—Twining stems. The one at the left (*Pharbitis*), a member of the morning glory family, twines counter clockwise, while that at the right (*Myrsiphillum*) twines clockwise, right handed, like the hop vine. (From Palladin, after Bonnier.)

its entire life cycle within a year. Biennials are those which require two years to complete a life cycle. Examples are the mullein, hollyhock, teasel, etc. Perennials live several to many years. After attaining reproductive maturity they may produce seeds or only spores annually.

Herbaceous stems are those which do not become woody. The aerial branches of herbaceous perennials may die down each year.

The structure and habit of the stem depend also upon whether it grows above or under the ground. Those which maintain an upright position in the air without support from some other source are mechanically strong like a pillar or column, as is the case with large trees; others combine certain rigidity with great flexibility, as in the cereals. Wheat and rye sustain a very heavy load at the tip of the stem. In proportion to their height and diameter such stems combine unusual strength with great flexibility.

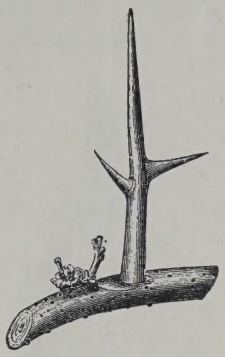
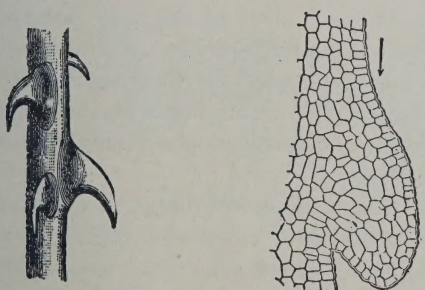


FIG. 120.—Piece of twig of honey locust (*Gleditschia tricanthos*) bearing a thorn, which is a modified stem. (Strasburger, Macmillan Co.)

Many of the special functions of stems are similar to those of the leaves, falling in the classes of support, protection, propagation, etc., together with other functions of a different nature.

Stem Tendrils.—The stems of many plants being very long and slender are unable to support themselves in an upright position. They clamber or climb upon other plants or other objects by means of leaf, stem or root tendrils or holdfasts. Familiar examples are grape vines, the great lianas of the tropics, wild cucumber, Bryonia, passion flower, Virginia creeper, etc. The method of attachment to the support is the same as that described for the leaf in the preceding chapter.



A B

FIG. 121.—A, prickles on stem of rose; B, a longitudinal section through a very young prickle, showing how the tissue beneath the epidermis enters into the structure of the prickle (emergence). × 200. (After Frank.)

The wild grape vine may attain a very large size, a foot or more in diameter, and a length reaching to the top of large forest trees where the leaves of the vine may completely cover those of the tree. A not uncommon sight in an open field or along the edge of a woods is a small tree completely hidden, as to its leaves and branches, by a wild grape vine. Sooner or later the supporting tree dies of starvation owing to the fact that its leaves, robbed of sunlight, are unable to manufacture sufficient food.

A different method of attachment from that of the twining tendril is found in the Virginia creeper (*Psedera quinquefolia*) and the Boston ivy (*Psedera veitchii*). These plants are able to cling to flat surfaces such as the side of a building or a tree trunk, by means of branched tendrils ending

in *holdfasts* (Fig. 118). The extremities of the tendrils are sensitive to contact with a surface, and they respond by sending outgrowths into the tiny crevices of the surface where such outgrowths become securely dovetailed or anchored.

Twining Stems.—A very different method of climbing is exhibited by twining plants, such as the morning glory, pole bean, and hop. Here the stem winds about a suitable support, either in the direction of the hands of the clock, *right twiners*, as in the hop, or, as a rule, counterclockwise, *left twiners*, as in the morning glory (Fig. 119). The twining is the result of a different kind of sensitiveness from that exhibited by tendrils. Experiments have shown that these stems twine as a result of the response to gravity, the same kind of sensitiveness as that which enables the root to grow down towards the center of the earth and the stem to grow upwards.

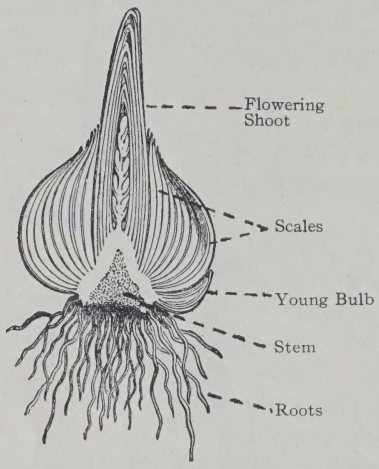


FIG. 122.—Flowering bulb of hyacinth in longitudinal section. The fleshy scales are the leaf bases of the last season's foliage leaves, which are converted into storage organs. Below at the right is a young bulb. (After Figurier.)

Thorns.—Stems which are modified into sharp pointed structures are known as thorns.* One of the most notable examples is the honey locust (Fig. 120).

It is not difficult to recognize the stem nature of the thorn, because of its direct continuation with the wood of the stem by which the thorn is borne and because upon young thorns rudimentary leaves are frequently developed.

Sharp pointed structures, often called spines or thorns, are found upon the stems and leaves of the blackberry, rose, wild smilax, etc. Such sharp pointed structures are *prickles* (Fig. 121, A). They should not be confused with spines or thorns. In the botanical sense prickles are *emergences;* they are developed as outgrowths of the epidermis together with a part of the underlying cortex. This fact is made clear by examining a young stage in development as shown in Fig. 121, B. Prickles usually snap off easily from the surface of the part of which they are outgrowths.

* In this book the terms *thorn* and *spine* have a structural significance, the spine signifying a sharp pointed structure which is a *modified leaf*, while thorn refers to a similar weapon of defense which is a *modified stem*. We do not have, on the contrary, separate words for the clinging organ, consequently it is necessary to use the expression *leaf tendril* when that structure is a modified leaf, and *stem tendril* when it is a modified stem.

The Bulb.—Many stems are so developed as to function both as organs of propagation and food storage. Many are adapted to a subterranean habitat. The more familiar are the *bulb*, *corm*, *rhizome*, and *tuber*.

A bulb consists of a short, flat or conical stem bearing thick, fleshy, overlapping scales which are modified leaf bases rich in stored food (Fig. 122). Bulbs bear both terminal and axillary buds.

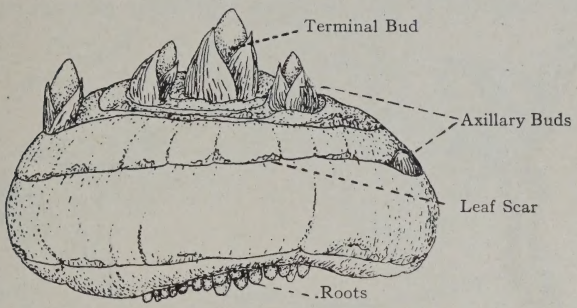


FIG. 123.—Corm of Gladiolus after roots have just begun to grow.

In the flowering bulb of the tulip or hyacinth, the terminal bud consists of the undeveloped, leafy flower-bearing shoot which will appear above the ground in the blooming season. The scales of the Madonna lily, if kept covered in moist sand will develop new bulbs at their bases.

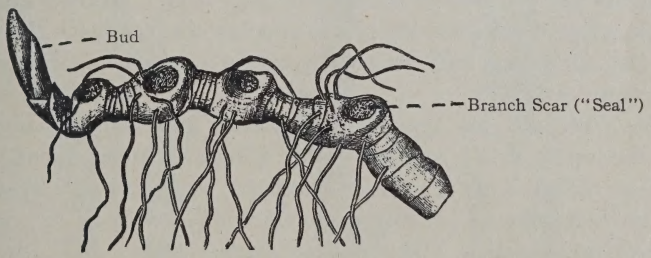


FIG. 124.—Rhizome of Solomon's Seal (*Polygonatum multiflorum*). Note the large branch-scars, "*seals*," left by the fallen aerial shoots. Each scar indicates a year's growth of the rhizome. (Strasburger, Macmillan Co.)

Corm.—The corm is found in the Crocus, Gladiolus, Indian turnip, etc. (Fig. 123). It is a short, solid underground stem covered by thin membranous leaf bases. Corms may bear both terminal and axillary buds.

Rhizome, Rootstock.—A rhizome is generally a thick, fleshy stem burrowing beneath the surface of the soil (Fig. 124). It bears scale leaves at the nodes and sends up aerial branches. Examples are found in the Solomon's seal, May apple, Iris, and maidenhair fern. In the winter,

or dormant condition, the growing end of the rhizome of Solomon's seal, for example, ends in a large bud which will develop into the tall shoot appearing above ground the following season. At the close of the season this shoot dies and falls away leaving a large scar or "seal."

Stolon or Runner.—A not uncommon modified stem is the long slender runner, or *stolon*, which creeps upon the soil or frequently beneath the surface. Its function is that of rapid vegetative propagation. One of

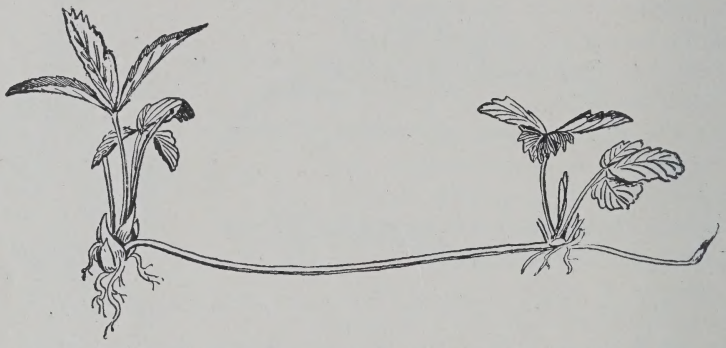


FIG. 125.—Portion of a strawberry plant, showing a runner which has developed a new plant at a node, and the new plant in turn has sent out another runner. (After Seubert.)

the most familiar examples is the strawberry vine, which may take root at the nodes and give rise to new plants (Fig. 125). Runners are present in a wide range of seed-bearing plants and in some ferns as in the varieties of the familiar house fern, frequently referred to as the "Boston fern" (*Nephrolepus exaltata*).

Tuber.—Perhaps the most widely known stem modification is the tuber, the thick fleshy stem growing above or under ground, which bears very small scale leaves and axillary buds called "eyes" (Fig. 126). It functions as a storehouse for food, and as an organ of vegatative propagation. The white potato plant, or Irish potato, (*Solanum tuberosum*), bears beneath the soil slender stolons whose growing ends enlarge into the tubers. Here we have a stem branch changed into both runner and tuber. The very small scale leaves borne by the runner and by the tuber may be seen if one carefully removes the earth from a "hill" of potatoes just as the tubers begin to develop.

The Cladodium.—A cladodium is a green stem which performs the functions of both stem and foliage leaves. Examples are Cacti, such as the "prickly pear" cactus, and the garden Asparagus. The leaves of such plants are transformed, as a rule, into scales or spines. The fine neddle-like shoots of garden Asparagus are stem branches and not leaves. Cladodia are developed in plants which live in dry or desert localities,

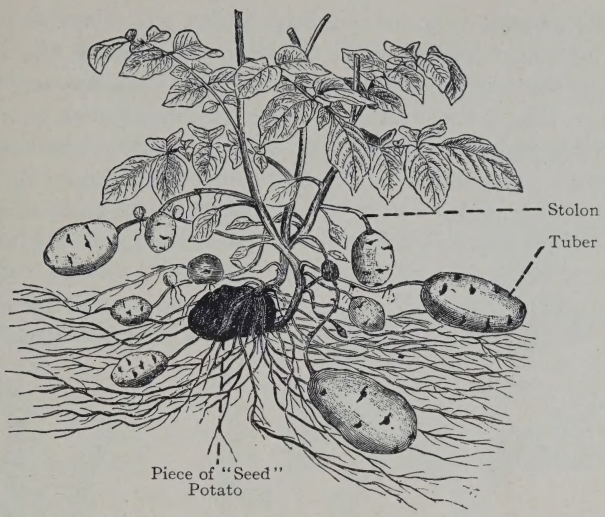


FIG. 126.—Lower part of a potato plant (*Solanum tuberosum*). The dark object is the piece of "seed" potato which was planted in the ground. Note that the tubers are formed at the ends of slender stolons. (Strasburger, Macmillan Co.)

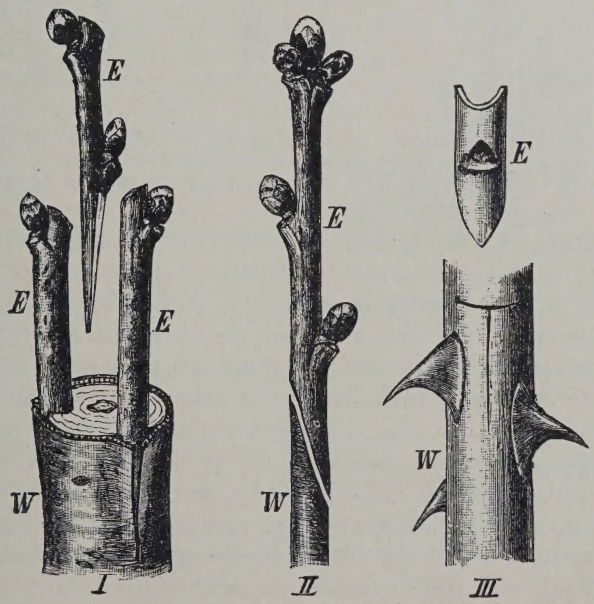
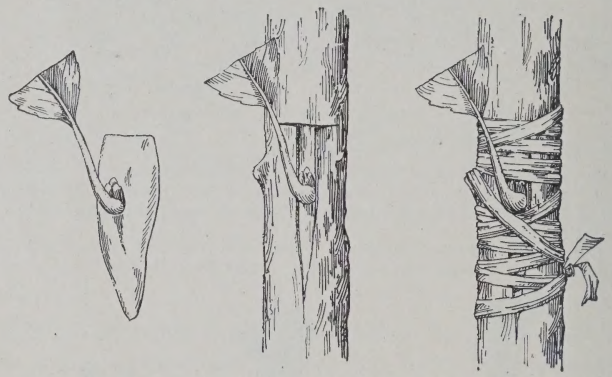


FIG. 127.—Various methods of making unions in grafts. I, crown grafting. II, splice grafting. III, budding. E, represents the scion and W, the stock. (Strasburger, Macmillan Co.)

where moisture is very limited in quantity and where the evaporation of moisture must be reduced to the minimum. Stems of plants living in marshy places may also develop cladodia, where, because of the nature of the soil, the plants absorb a relatively small quantity of water.

Grafting and Budding.—Many different kinds of plants may be combined into a single individual by a process carried out by man, known as grafting. The piece of stem to be grafted is the *scion*, and the rooted plant to which it is united is the *stock*. Making a graft is bringing the cut surfaces of stock and scion together in such a manner that like parts which are alive, especially the cambiums, are in close contact, and then binding the two with raffia, grafting wax or some other method of support



A B C

FIG. 128.—Method of budding. A, a bud cut from a twig of the desired plant, with a piece of the bark and underlying wood. B, the bud inserted into the T-shaped slit in the bark of the stock. C, the same with the bark bound in place by strips of raffia. (Bowden.)

and protection until the tissues of stock and scion are grown together. Methods of making graft unions are illustrated in Fig. 127.

Budding, a form of grafting, consists of cutting off from the desired plant an uninjured bud with a little of the bark and underlying young wood and inserting it under the bark of another plant (Fig. 128). If the operation be performed correctly and at the season when the cambium is active, the bud will soon be united with the wood and bark of the stock. Peaches, apples, oranges, roses, and a very large number of economic plants are propagated by budding and by the other methods of grafting. This method, like all other methods of vegetative propagation, is a sure way of securing plants which will be more exactly like the desired parent plant in flower and fruit than can be secured from seeds. The stem developing from the graft or bud is usually the only one permitted to develop on the stock, unless more than one kind of flower and fruit is desired upon the same tree.

Inarching.—Inarching, or approach grafting, is accomplished by bringing suitably prepared surfaces of stock and scion in close contact while both plants remain rooted till union is complete, when the base of the potted scion is cut away (Fig. 129).

Propagation by Cuttings.—Stems lend themselves to another method of artificial propagation which is used perhaps more extensively than is grafting. This consists in severing a branch, "cutting," from the plant and placing the lower end in a suitable soil or in water until adventitious roots develop sufficiently to maintain the cutting as a growing individual when set out in a proper environment. Fastening a branch down upon the soil so that roots and shoots will develop from it is a practice known as *layering*.

FIG. 129.—Inarching or approach grafting. The potted plant will supply the scion. (After Figuier.)

TOPICS FOR REVIEW AND DISCUSSION

Do you know of any stems which do not end in a bud as defined in the text?

Explain how such leaves as the buckeye, horse-chestnut, etc. fall from the stem.

Why do many dead leaves of oak and beech remain on the tree all winter? Why do they fall just before the new leaves come out?

Is the absciss layer formed outside or inside the cork layer?

Do the silky hairs found in buds keep the inner parts from freezing in very cold weather?

In what sense are all buds terminal buds, although not so designated?

Are dormant and latent buds of value to the plant? Cite illustrations and conditions to support your answer.

What makes the end branches of the lilac fork?

Has a scaly bud like the hickory bud any advantage over a naked bud, like that of sumac?

Are buds present in the axils of the leaves of Indian corn?

Name some plants composed wholly of mature primary tissues when fully grown.

What is protoxylem? Protophloem? Why are protoxylem elements composed largely of spiral or annular vessels?

What is a tracheid? What are tracheae or tracheal tubes? What is a pitted tracheid? A spiral tracheid? A scalariform tracheid? Do these terms apply to vessels as well as to tracheids?

How are tracheae or tracheal tubes formed from two or more cells?

In what class of seed plants are tracheal tubes absent?

Why does the wood of a tree, such as the elm and oak, appear in concentric rings?

Why are these rings called annual rings? Are two rings ever formed in one year?

Why are annual rings not recognizable in the phloem?

Why is the bark of an old tree (200 years or over) not as thick as the wood?

Does the pith increase in size and bulk as the tree grows older?

If a branch is five feet from the ground when the tree is five years old, is the same branch higher from the ground when the tree is ten years old? Why?

What is heart wood and sap wood? Which is changed into the other? What constitutes the change?

What trees make the most durable fence posts without chemical treatment?

Where does a fence post rot off first?

What is the chief cause of the decay of wood?

What do lumbermen mean by "silver grain" of wood?

How must a log be sawed to secure quartered lumber?

What is edge-grain flooring?

Why is ebony black and juniper or wild cherry reddish?

What is a knot?

What is a dry knot? A live knot?

Why do trees grown in the forest have tall trunks which yield clear lumber, while those grown in the open field have large branches nearer the ground and yield poor lumber?

Girdling by removing a ring of bark may kill the tree slowly. Why? Why will girdling by removing a ring of wood two or three inches deep in the summer cause the leaves to die in a short time?

Would you try to kill a palm tree by girdling it as in the case of an elm?

Do trees evaporate water in the winter?

Of what value are lenticels to a stem?

What tree produces commercial cork? What cork is of the best quality? From what countries do we secure most cork? Why does birch bark come off in thin sheets?

What is latex? What garden vegetables have latex?

In what structures do rubber-trees produce rubber? In what form does the rubber come from the tree?

Whence comes the milk found in the milkweed?

Whence comes the resin of the pine tree? What is amber?

Is resin of any value to pine trees?

How does a monocot stem increase in diameter?

Why is a white (Irish) potato tuber a stem and not a root?

Pole beans and peas climb upon supports. How does each do so?

How does the Virginia creeper cling to a wall?

Morphologically what is the difference between spine and prickle?

What members of the plant may become thorns as the term is defined in the text?

What kind of buds occur upon rhizomes?

Is it correct botanically to speak of a crocus, canna, dahlia, or gladiolus as a bulb? Why?

Explain some different methods of grafting. In making successful grafts what tissues must be held in direct contact? Why?

What is callus or wound wood?

Explain how large wounds "heel" over.

How are wounds healed in leaves?

What two parts make up an annual ring? How do these two parts differ? What is the function of each part?

In a cross section of a linden stem four or five years old, can you tell how much came from one vascular bundle?

Distinguish between *the* cambium and *cork* cambium.

Why does not the bark of a beech tree flake off like that of the maple or elm?

Distinguish between, spine, thorn, and prickle.

How many different kinds of modified stems does the white potato (*Salanum tuberosum*) bear?

What is meant by the expression "flowering bulb" and "flowering corm"?

What method of grafting do you think would be most successful on young stock?

CHAPTER V

THE ROOT

General Characteristics.—Typical roots, which grow in the soil, are similar in appearance even in those plants which show the greatest contrast in the character of their stems. The two main functions of roots are anchorage and the absorption of water and dissolved substances from the

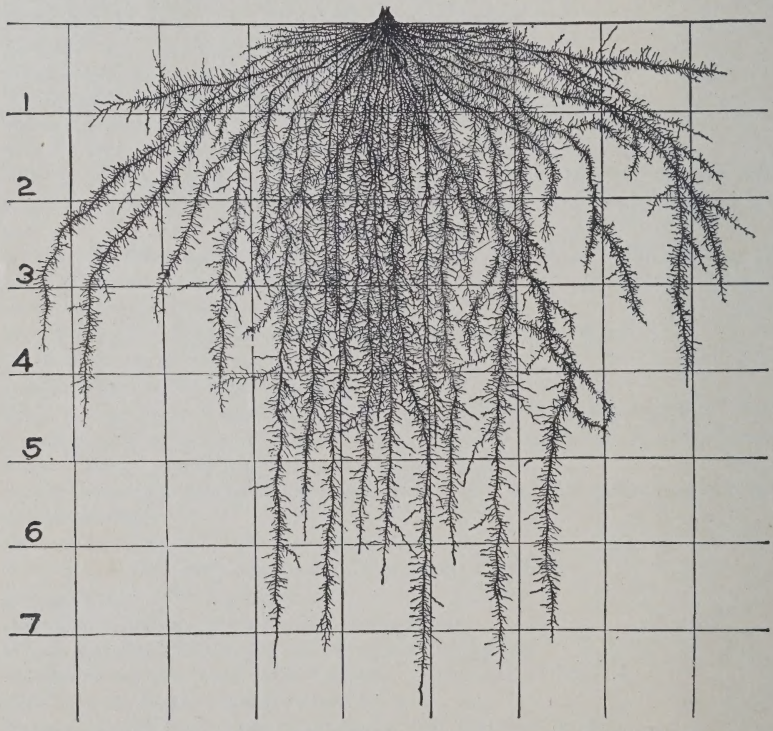


FIG. 130.—Root system of Iowa Silver Mine Corn 116 days old, showing the extensive development of the root system. The squares represent a scale of one square foot. (Gager.)

soil. A root differs from a stem in that the root does not bear leaves; it is not differentiated into nodes and internodes, and its growing point is covered by a root cap.

The root system in the ground spreads downward and outward as the stem system extends upward and outward (Fig. 130). Owing to irregulari-

ties in the soil the spread of the root system is much less regular than that of the stem. In some plants like the oak, hickory, and black walnut, the roots penetrate deeply into the ground, while the beech is a shallow rooted tree. The frontispiece of this book represents a large beech and a sugar maple each over two feet in diameter, growing almost in contact side by side. The roots of the maple penetrate to a greater depth in the soil, so that the two trees do not suffer because of root competition.

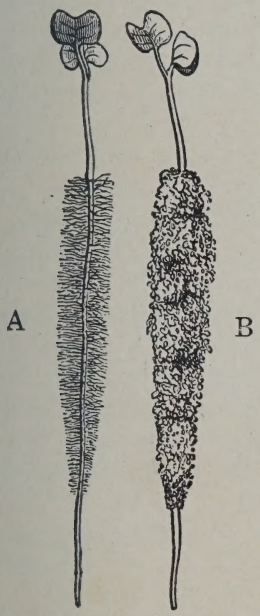


FIG. 131.—Seedlings of radish. A, grown in moist air; B, in soil. (After Sachs, "Lectures on the Physiology of Plants," Clarendon Press.)

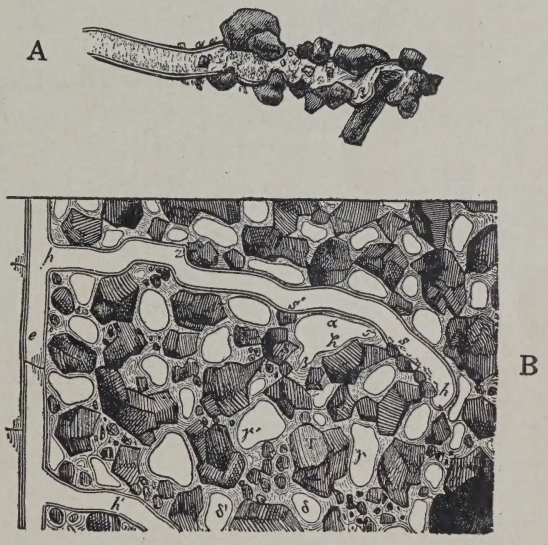


FIG. 132.—Relation of root hairs to the soil. A, end of root hair with adhering particles of soil. B, diagram of soil penetrated by root hair; soil particles (dark) surrounded by films of water (curved parallel lines); air cavities are white. (A, Strasburger, Macmillan Co.; B, after Sachs.)

Under certain soil conditions the roots of cereal crops, wheat, corn, oats, may penetrate to the astonishing depth of six or seven feet (Fig. 130).

The tender growing ends of roots are smooth and white in color. Just back of the smooth end is a region richly provided with epidermal outgrowths, *root hairs*, which are in very close contact with soil particles (Figs. 131, 132). Old roots are usually brown in color. Root hairs are usually unicellular and of short duration. As the root becomes older the hairs die, and new ones are ever being produced upon the progressively younger regions of the growing end. In certain forest trees the root hairs are multicellular, and they may remain functional for a long time.

The young tender end of the root consists of the following regions: the extreme tip is the root cap; back of the center of the root cap is the embryonic tissue of the root proper which gives rise to the cells of the

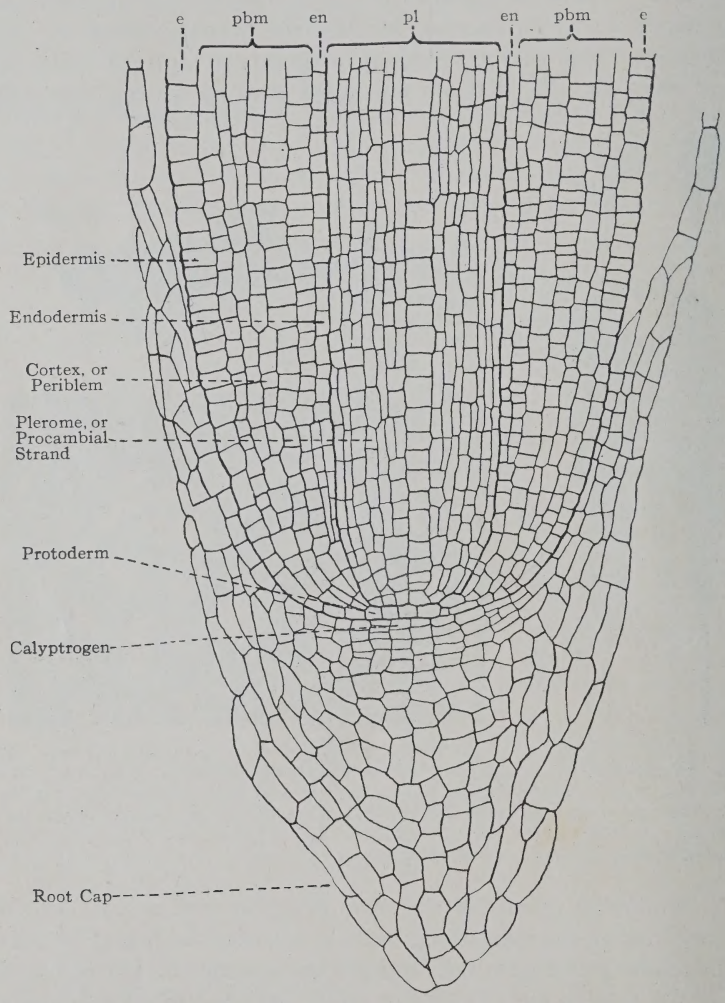


FIG. 133.—Longitudinal section through the root tip of the Spiderwort (*Tradescantia*). *pl*, vascular cylinder, or plerome; *pbm*, cortex, or periblem; *e*, epidermis; *en*, endodermis.

epidermis, cortex, and vascular cylinder; back of the embryonic region is the region of rapid elongation, the smooth stretch of the root, and beyond this, the region of root hairs, and finally the maturing tissues (Fig. 131).

The Growing Point of the Root.—The origin and arrangement of the several parts in the tip of the root are readily seen in a longitudinal section (Fig. 133). Here we see the root cap fitting over the end of the root proper like a thimble upon a finger. In many roots a sharp boundary line is visible between the growing point proper and the root cap. The meristem (calyptrogen) from which the cells of the root cap are replenished lies at the base of the cap just outside the line of demarcation. In some roots, such as that of the pea (Pisum), there is no sharp boundary between root cap and the tissue back of it. The oldest cells of the cap are injured and destroyed as the result of injury in the soil caused partly by the pressure of the elongating root; or they may slough off normally.

The primordial tissue of the rounded growing end is confined to a small region at the extreme tip, not exceeding two or three layers of cells in thickness. This region gives rise to the protoderm, the cortex or *periblem* (*pbm*), and the procambial cylinder, *plerome* (*pl*). The *endodermis* (*en*) is derived generally from the cortex.

Back of the meristematic tissue is the region of elongation and still farther back is the region of maturation or internal development. Root hairs are developed from the epidermis. These begin in the region of elongation and reach their full development a short distance in the maturing region. In older parts of the root, the root hairs die and disappear. Root hairs live a comparatively short time, however. As the old die, new hairs are constantly being produced towards the tip. With progressive growth of roots, the absorbing surface is brought constantly into new regions from which water and mineral elements are secured.

In some trees the root hairs are multicellular, and they may remain functional for a longer time than in the majority of plants.

Structure in Cross Section.—In a cross section through the mature root, the three parts are readily recognized; the *epidermis*, the *cortex* and the *vascular cylinder* (Fig. 134). The central cylinder of the root of an onion, for example (Fig. 135), is surrounded by the endodermis, whose radial walls are thickened (Casparian strips or thickenings). Beneath the endodermis is the pericycle. The vascular tissue consists of a circle of six masses of phloem alternating with six masses of xylem. In passing from stem to root the strands of phloem and xylem shift, so that they lie tangentially side by side. This arrangement of phloem and xylem in the vascular region is known as the radial type of bundle. In roots of certain plants there is a central pith.

The protoxylem is next to the pericycle. Proceeding toward the center from each mass of protoxylem we find a scalariform vessel (*sc'*) six in all.

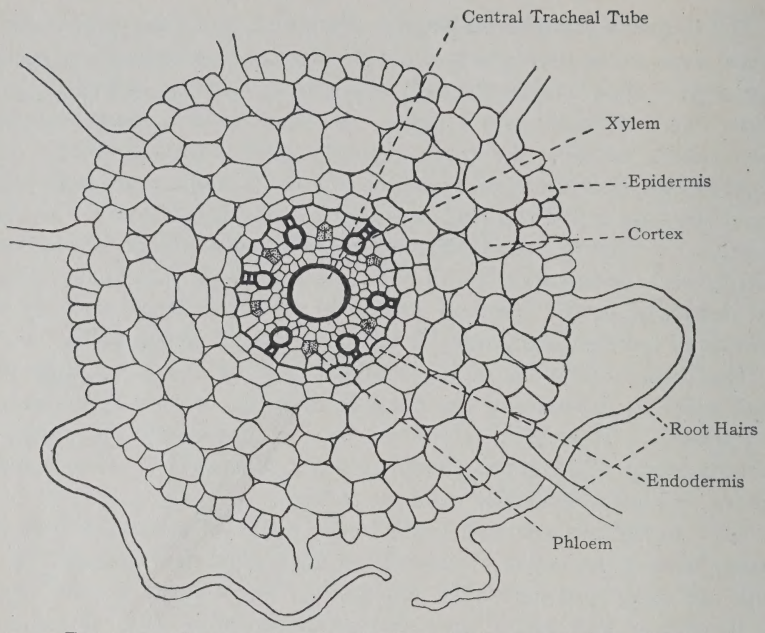


FIG. 134.—Cross section of a small root of a monocotylous plant.

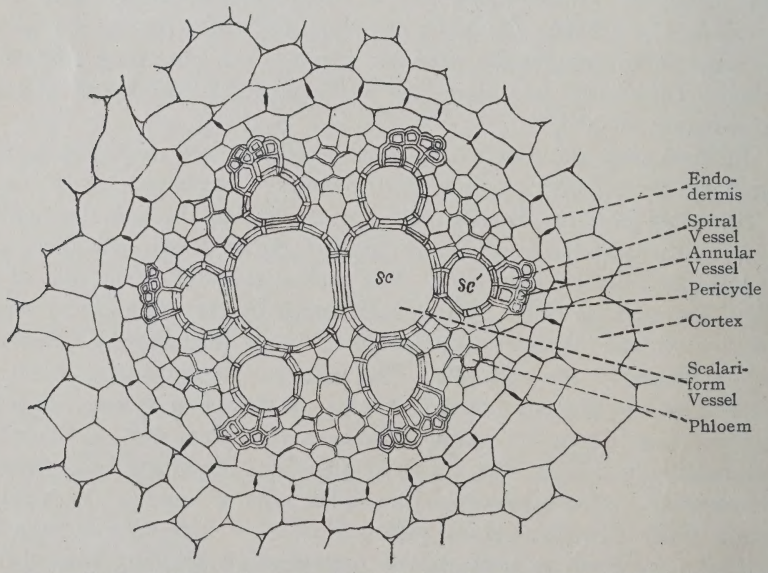


FIG. 135.—Cross section of the central cylinder of the onion root (*Allium cepa*) with a few cells of the cortex.

In the center are two large scalariform vessels (*sc*).

In Fig. 136 is shown the mode of origin of secondary roots, or root branches. The microscopic details are illustrated in Figs. 137 and 138. The growing point of the secondary root arises from the pericycle. It will be seen that the primordium of the young root crushes first the endodermis (Fig. 137, A, B) then breaks its way through the cortex (Fig. 138). The

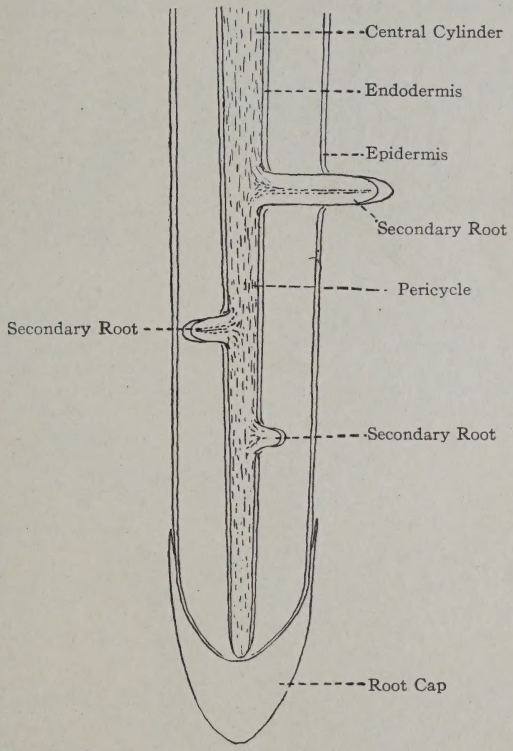


FIG. 136.—Diagram of a longitudinal section of the end of a root, showing the origin of root branches from the central cylinder.

phloem and xylem of the young root connect histologically with phloem and xylem of the old root.

Secondary Thickening of Roots.—Roots of most dicotylous plants thicken by means of secondary growth as do the stems. A cambium arises between phloem and xylem (Fig. 139). At first it follows a very undulating course around in the vascular cylinder. It passes, for example, along the inside of a mass of phloem, then radially outwards between phloem and xylem, thence with a short curve in a tangential direction along the outer edge of the protoxylem, continuing with another sharp curve radially

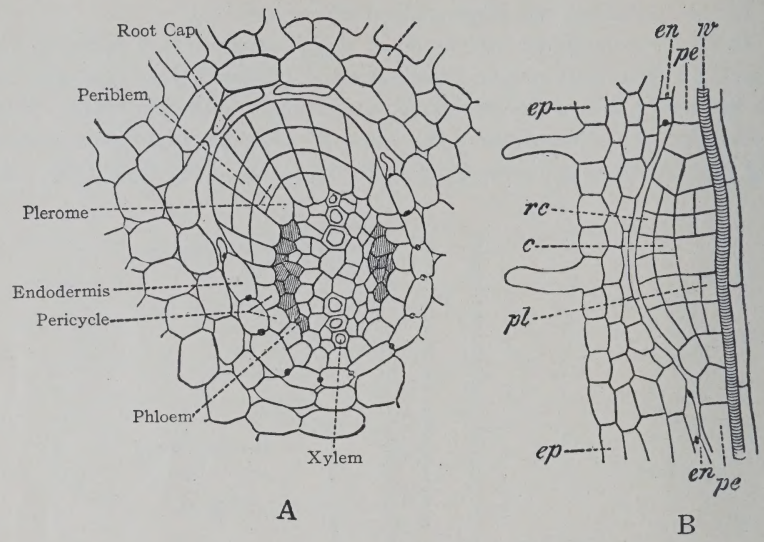


FIG. 137.—Illustrating origin of secondary root in seed-bearing plant. A, cross section. B, longitudinal section; *ep*, epidermis; *en*, endodermis; *pe*, pericycle; *c*, cortex; *rc*, root cap; *pl*, plerome; *w*, vessel. (After Van Tieghem.)

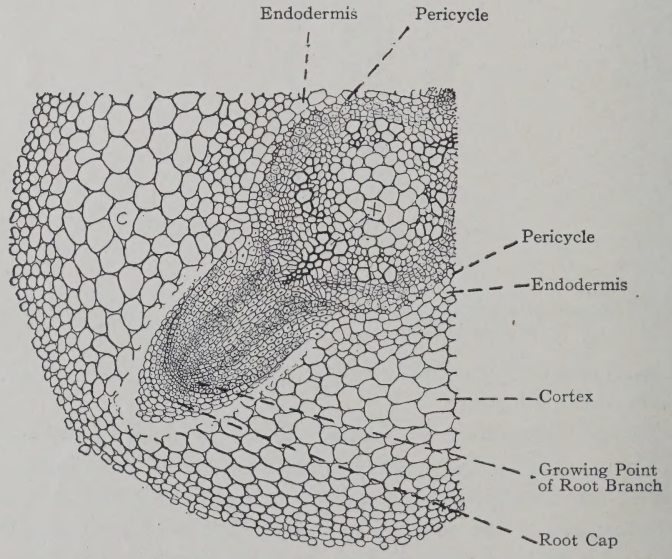


FIG. 138.—Cross section of root of lupine, showing root breaking through cortex. (From Curtis.)

inwards between the next two masses of phloem and xylem, and so on until the zone is complete. The cambium ring being complete, new phloem is added on the side of the phloem and new xylem next to the xylem and pith. Rays are also developed in the secondary layers. Consequently annual rings of wood and bast are developed in older roots as in the case of stems (Fig. 140).

As certain roots grow old and the secondary thickening just mentioned is well under way, a *cork cambium* is established in the pericycle, which

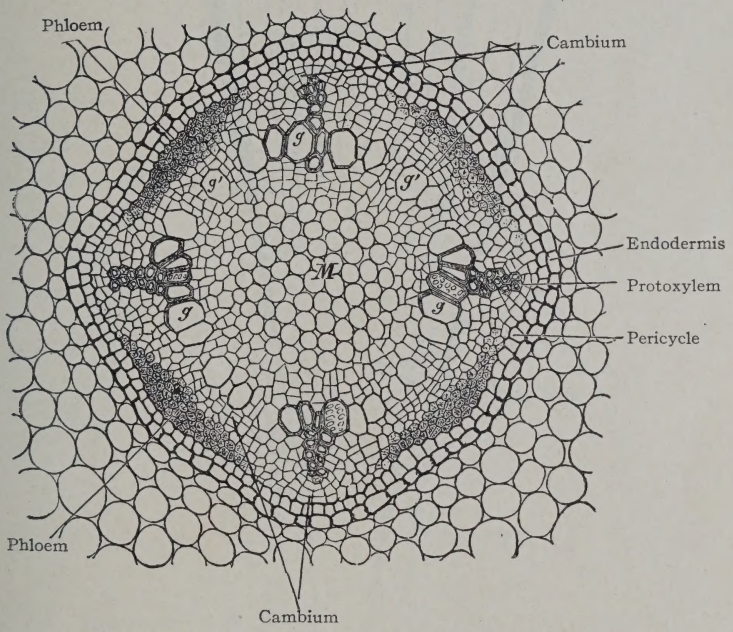


FIG. 139.—Cross section of the vascular cylinder with a few surrounding cells of the cortex of the root of the bean (*Phaseolus multiflorus*) soon after secondary thickening has begun. (From Sachs, "Lectures on the Physiology of Plants," Clarendon Press.)

produces cork on the outside and adds to the secondary cortex on the inside. After the production of the layer of cork, the primary cortex dies and eventually disappears (Fig. 140).

Anomalous Thickening of Roots.—In such roots as the beet, several cambium rings arise in succession outside the original cambium, in the ground tissue. Each of these cambiums functions for a time, producing phloem and xylem, but the elements usually consist of thin-walled vessels and parenchyma in which food is stored.

Root of the Fern.—The root of the fern is built on the same structural plan as those of other plants with this notable exception, that the primordial meristem consists of a single *apical cell* in the form of a tetra-

hedron or triangular pyramid, whose base faces the root cap (Fig. 141). By successive divisions this apical cell cuts off segments, new cells, from all four faces. The cells cut off from the base produce the root cap, those from the three lateral faces, all the rest of the root. From each lateral

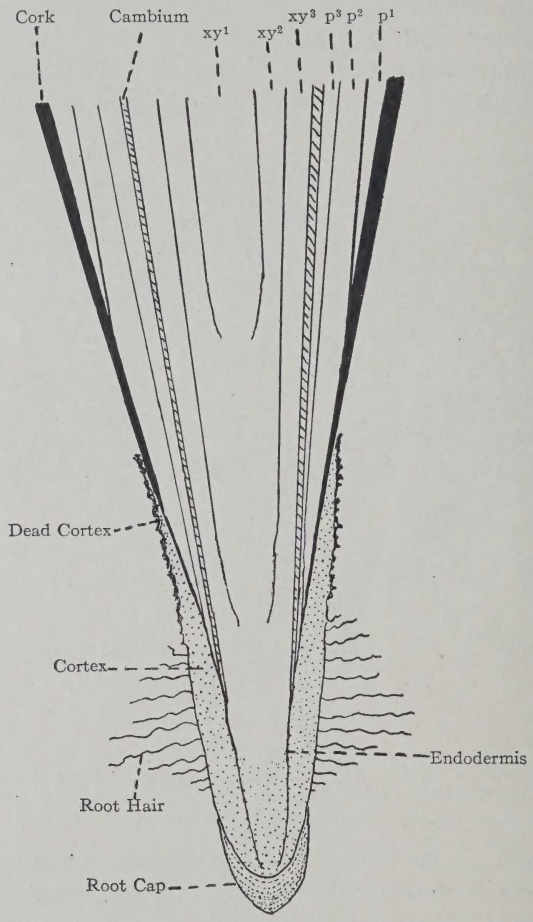


FIG. 140.—Diagram of a longitudinal section of a root, showing secondary thickening and the disappearance of the cortex. Endodermis becomes surface layer beneath which is formed the cork from the pericycle. p^1, p^2, p^3, phloem formed during first, second, and third years; xy^1, xy^2, xy^3, xylem formed during first, second, and third years.

cell will be formed inner and outer cells. The outer cells give rise to the protoderm and cortex which may include the endodermis. The inner cells produce the procambial cylinder. The cell divisions follow in regular sequence, the apical cell enlarging a little after each division. The cell divisions in the fern root tip are so regular that the origin of epidermis,

cortex, endodermis and central cylinder may be traced with accuracy from the apical cell.

The Stele and the Vascular Bundle.—The vascular cylinder in a root or a stem is referred to as the *stele*. A stele, which may consist of one or

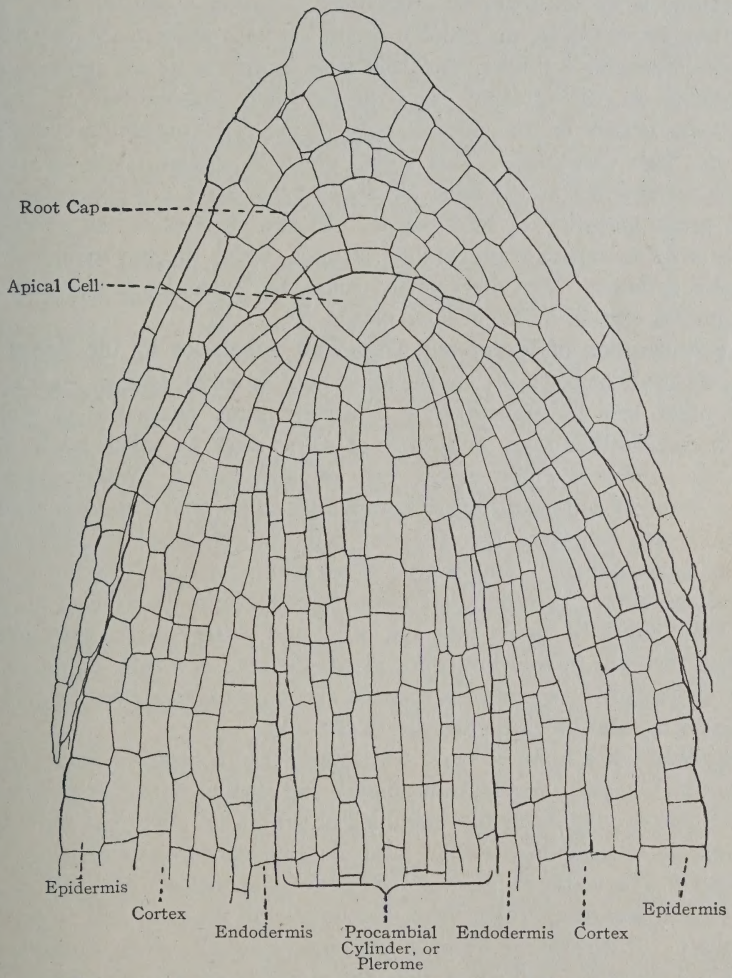


FIG. 141.—Longitudinal section through the root tip of Adiantum.

more vascular bundles, represents all the vascular tissue developed from a procambial strand. In the growing end of the root, for example, the narrow elongating cells of the central cylinder constitute the procambial strand of the root, and the vascular tissue derived therefrom is the stele.

In the ferns, for example, there are three principal types of stele: (1) the *protostele*, (2) the *siphonostele*, and (3) the *polystele*, or the dissected siphonostele, the *dictyostele*. The protostele consists of a single solid cylinder of xylem surrounded by phloem, as in the root. The protostele is regarded as the most primitive development of vascular cylinder. The siphonostele is in the form of a cylinder enclosing a central pith. In Adiantum, for example, the phloem occurs on both sides of the xylem in the pith-containing cylinder, and this stele is known as an *amphiphloic* siphonostele, as distinguished from the *ectophloic* siphonostele, in which the phloem occurs on the outside only of the pith-containing cylinder, as in the fern Osmunda. This stele, which is composed of collateral bundles, is regarded as the most advanced type, since it is characteristic of the great majority of seed plants. In the dictyostele the vascular bundles arise in separate procambial strands, which are not arranged in a definite cylinder. The dictyostele occurs, for example, in the stem of Pteris and in certain monocotylous plants (Fig. 115).

The Absorption of Water and Dissolved Substance by the Roots.—Inasmuch as about 50 to 98% of the plant body is water, and, as the leaves of the plant lose by transpiration relatively large quantities of water daily, it follows that large quantities of water must be taken up by the roots, the source of entry in the case of land plants. Water, carbon dioxide, mineral salts, and other compounds from which food is made, and which are necessary for all living cells, are obtained by the plant from its surroundings. This is true of all plants whether they do or do not possess roots. In order that these materials may be utilized by the plant, they must be taken into the cells, and, furthermore, they must pass into the cells in solution, since plants do not, as a rule, ingest solid bodies. We shall now consider some of the physical processes by which substances in solution gain entrance to the cells.

Diffusion.—If a lump of sugar be dropped into a vessel of water, after a short time the lump will become smaller and smaller until it is no longer visible. We say the sugar has dissolved in the water. By that we mean the particles of sugar in the solid lump became scattered or dispersed in the water. The water at the surface in the glass will not taste sweet at first, while a few drops taken from the bottom of the glass will be found very sweet. If we stir the water it will become equally sweet throughout almost immediately, indicating that the sugar is equally distributed or diffused in the water. The sugar will become evenly diffused in the water in time even though the water remain perfectly quiet. The particles of sugar disperse in all directions with or against the pull of gravity and without the aid of energy from the outside. We cannot see the sugar because the particles are too small. The particles or molecules of sugar

are dispersed among the molecules of water. Now, a molecule of sugar, or of any other substance, is the smallest particle into which the substance can be divided and still continue to be that substance. If the molecule of sugar be divided, the resulting particles are not sugar but something else. Molecules are so small that nobody has ever seen one, yet we know perfectly well that they exist. However, their weight and size have been computed. In solutions such as this, the substance dissolved is called the *solute*, and the water is the solvent. In a solution of sugar, the sugar is the solute and the water is the *solvent*. Now, particles of gases, such as carbon dioxide (CO_2), will also diffuse among particles of water and among particles of other gases.

There is another kind of diffusion by which a piece of dry wood, gelatin, glue, dried apple, seeds, etc., absorb water, which is known as *imbibition*.

Osmosis.—In order that water and solutes may enter the cell they must first pass through the cell wall and through the plasma membrane just inside the cell wall. The diffusion of water and solutes through a membrane is known as *osmosis*. Inasmuch as osmosis is so important to plant life, as well as to all other life, it is necessary that we acquire an elementary understanding of this process. To do so we perform a simple experiment and observe the results. A diffusion shell is filled with molasses and closed by a perforated rubber stopper into which a glass tube is thrust. The shell is now immersed in a vessel of water and held in position by a support (Fig. 142). The molasses is merely a convenient sugar solution. The shell is a membrane between molasses and water. In a short time we observe that the molasses, or a mixture of molasses and water, will rise in the glass tube and continue to rise for some hours. As water continues to osmose into the shell, the shell becomes much distended by the pressure, and this pressure is known as *osmotic pressure*. The osmosis causes the water, or the mixture of water and molasses, to rise in the glass tube. As long as osmosis continues, the column will continue to rise in the tube.

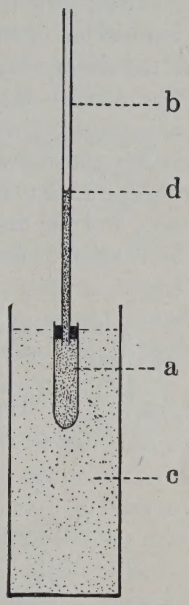


FIG. 142.—Apparatus demonstrating osmosis. *a*, diffusion shell filled with sorghum molasses, and closed with a perforated stopper. The shell is firmly tied to the stopper by means of a waxed string; *b*, glass tube thrust through stopper; *c*, jar containing water; *d*, height of liquid in tube.

In order that water may pass through the membrane, it must first enter the membrane, i.e., it must wet the membrane. Water wets the membrane, because it is soluble in the membrane. The water passes out

of the membrane into the molasses, because the molasses has a greater attraction (affinity) for the water than has the membrane.

If we examine our apparatus after some hours, we shall find that some of the molasses has diffused out of the shell into the water of the jar. The molasses, like the water, wets the membrane, and some of the sugar osmosed out of the membrane into the water, because the sugar was soluble in the water which had been taken up by the membrane. In our experiment osmosis takes place into the shell and out of the shell. The greater movement is toward the side of the membrane wetted by the solution of greater concentration. So long as the solution in the shell remains more concentrated than the solution outside of the shell, water will rise in the tube, and the osmotic pressure will continue to increase. When the rate of diffusion in both directions becomes the same, the osmotic pressure no longer increases. Different substances generate different degrees of osmotic pressure. Common salt will produce a greater osmotic pressure than grape sugar, and grape sugar a greater pressure than cane sugar.

Let us now turn our attention to the living plant cells in which osmosis is carried on. The cell wall of a tender cell is a cellulose membrane which corresponds to the diffusion shell of our experiment. In the living cell, however, there is another membrane, just within the cell wall, which consists of living protoplasm, the *plasma membrane.* It lies in contact with the cell wall. This membrane is not present in our apparatus. The contents of the live cell within the plasma membrane correspond to the molasses. Water osmoses into the cell in a manner similar to that into the shell containing the molasses. As in the shell, the greater movement is toward the side of the membrane wetted by the solution of greater concentration. As the cell contents have a greater concentration than the surrounding water, osmosis takes place into the cell, and osmotic pressure is set up. The osmotic pressure keeps the cell distended and firm. In tissues with thin tender cell walls the osmotic pressure, by keeping the cells distended (turgid), enables those parts to remain firm and to keep their normal shape, as in the case of leaf blades and stems without much wood or strengthening tissues. In the absence of osmotic pressure such parts will wilt.

Under certain conditions the osmotic pressure may become so great as to burst the cells. This happens in certain cases to pollen tubes when grown in water, and to some fruits, such as plums, which burst because of the high osmotic pressure in the cells.

There is a profound difference between a living membrane and a dead one as regards osmosis. A simple experiment will illustrate in a way this difference. A few slices of a fresh, red beet are washed in cold water several minutes to remove the color which escaped from the injured cells.

The slices are now permitted to remain in clear water. They will retain their color, and the water will remain clear. If the water containing the slices be now heated to boiling, it will become red almost immediately, owing to the fact that the red pigment, which was dissolved in the cell sap of the beet cells, diffused out readily through both plasma membrane and the cell wall. Heating killed the plasma membrane. The living membrane did not permit the color to diffuse from the cell; it tended to regulate osmosis. The living membrane has the ability to determine in a measure what may pass into the cell and what may escape from it. This ability is referred to as the selective power of the cell. The cell has the ability to change its osmotic power under different external and internal conditions. One of the most fundamental properties of the living plasma membrane is its ability to be permeable to water and at the same time less permeable to solutes.

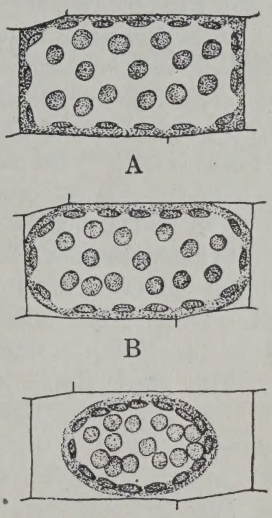


FIG. 143.—Plasmolysis of a cell. A, normal cell. B, plasmolysis has begun. C, completely plasmolyzed.

This selective power, which is of great value to the plant, is shown by the fact that the roots of different kinds of plants may take up from the soil entirely different compounds. One kind may absorb more lime, another common salt, another potassium, etc. The selective power is shown in a marked degree by such plants as the brown seaweeds. From a medium, sea water for example, containing about 3% common salt, a much greater quantity of potassium is accumulated in the plant than is sodium. For the same reason, iodine, which is present in sea water in very small quantities, is absorbed in proportionably larger amounts than other substances which are more abundant in the water.

Plasmolysis.—We may now note one of the results of osmosis in living cells under certain laboratory conditions. If cells of some suitable plant, such as Spirogyra, or the leaf of a moss, be mounted in water and observed with the microscope, the cytoplasm containing the chloroplasts is seen next to the cell wall as a thin layer, the center of the cell being occupied by a large vacuole (Fig. 143, A). A 7% solution of potassium nitrate is drawn under the cover glass. In a minute or two the cytoplasm will contract away from the wall, first at the corners, and tend to round up in the center of the cell (Fig. 143, B). Since the plasma membrane is more permeable to water than to the nitrate, some of the

water of the cell has passed out through the plasma membrane, and the cytoplasm has contracted away from the cell wall because of the diminished turgor. Owing to the elasticity of the cell wall, the size of the cell has also been reduced. Some of the cell sap and the potassium nitrate have accumulated in the space between the plasma membrane and the cell wall. The potassium nitrate passes more readily through the cell wall than through the living membrane. Cells in which the cytoplasm has contraced away from the cell wall even at the corners owing to the loss of water from the cell, are said to be *plasmolyzed.*

If the potassium nitrate be replaced with water, water will osmose into the cell, and the turgor will be restored, the cytoplasm moving back into the ends of the cell, provided the living substance was not killed or injured by the nitrate. In this experiment the direction of the greatest movement of fluid is towards the side of the membrane or membranes wetted by the solution of greatest concentration. It must be remembered that cells without visible vacuoles may be plasmolyzed.

Self-plasmolysis.—Self-plasmolysis is a normal function in plant cells during certain steps in development. In the reproduction of Spirogyra, for example, the cells that unite become plasmolyzed before union (Fig. 143, B, D). Plasmolysis cannot occur in a dead cell.

The Root Hairs in the Soil.—Let us now turn our attention to the root hairs which are the chief absorbers for the root, and think of them in their normal home, the soil, wending their way in a very irregular course among the soil particles as indicated in Figs. 131 and 132. The soil particles are very irregular in shape and size, and the spaces among them are also variable in shape and size. In growing through the soil the hairs become very crooked and irregular, now narrow, now wider, with straight stretches alternating with very crooked portions, in order to make their way through the open spaces. In drained soil each particle is surrounded by a film of water which adheres to the particle as water adheres to the surface of a bit of stone or to any surface. The films of water are dilute solutions of various substances, especially mineral salts, which the plant may absorb. The task of the root hairs is to absorb by osmosis the necessary water and the substances (mineral salts) dissolved in it. Here is where the selective osmotic power of the live cell comes into play. The task of absorption is a difficult one inasmuch as the osmotic power has not only to take up the water and dissolved salts, but it must also overcome the capillary force which holds the films of water to the soil particles. The concentration of the cell contents in the root hair must be maintained to such a degree that the water and salts will osmose into the cells. If the concentration of the cell contents of the hair should be less than that of the solutions in the soil,

water may diffuse out of the hairs, and injury will result. This happens when dry commercial fertilizer is applied to the soil in too large quantities. This fact may be clearly demonstrated if one places the roots of a seedling corn plant in a vessel containing a tolerably strong solution of common salt. The plant will wilt after a short time as if left with the roots exposed to the dry air of the room.

All of the live tender cells of the root surface absorb by osmosis, but the hairs increase the absorbing surface many fold because of their great number. It has been estimated that the root hairs increase the absorbing surface of the root twelve times or more.

The water and solutes absorbed by the hairs and other epidermal cells are passed on by osmosis from cell to cell of the cortex whose cells also have living contents. The innermost cells of the cortex give up water and solutes to the vessels* of the xylem, which have permeable walls but no living substance, and through these vessels the solutions pass upward through root and stem to the leaves. In a subsequent paragraph (on the ascent of sap in tall plants) we shall learn something about the way in which the water and dissolved solutes continue upward into the plant. Here we shall turn aside temporarily to examine more fully into the nature of the soil.

The Soil.—Soil is composed of powdered rock and humus. Humus is derived from decayed vegetable and animal matter. In addition to these particles there is water, air, and soil life. Soil water may exist in three conditions, (1) *gravitational* or free water, (2) *capillary* water, and (3) *hygroscopic* water. If soil be allowed to dry in the air, the air-dry soil will still contain moisture which can be driven off by heating. This is the hygroscopic water. An examination of moist, but well drained, soil will reveal the presence of the particles somewhat as shown in Fig. 132, B. In the larger spaces among the particles are air bubbles, shown white in the figure. Around each soil particle is a film of water, indicated by parallel lines. The films of water surrounding the particles constitute capillary water. This is the water available to plants which grow normally in drained soil. In securing the capillary water the osmotic power of the hairs must overcome the capillary force holding the films to the particles.

In the soil of a swamp or marsh, which is saturated with water, the air is driven out by the excess water. The white spaces in Fig. 132, B will be filled with gravitational water, so-called because it is readily removed by gravity when a suitable outlet is provided. Placing drain tile for drainage in wet or swampy ground is merely providing an outlet so that the free water may flow away under the force of gravity. Gravita-

* Just how this takes place is not well understood.

tional water is detrimental to plants whose roots are adapted to function in aerated soil.

As just stated, free, or gravitational water, is moved by the pull of gravity, and it goes downward until it reaches a point where the soil is saturated. This point is known as the *water-table*, or the location of permanent ground water. When the water of the water-table comes to the surface, a spring may be the result. The water table varies with the rainfall, rising in wet weather and falling in the dry season. In a swamp the water-table is at the surface.

Hygroscopic water is not affected by gravity or dryness. As stated above it is present in air-dry soil, such as the dust of a dry road, but it is not available to plants. Capillary water is not affected by gravity, but it moves from moist to dry places much as a drop of water moves through blotting paper or the oil through a lamp wick. Dissolved plant food is brought up from the subsoil by capillary water. The alkaline character of certain soils is due to this fact. By capillary means, water will rise six to ten feet higher in such fine-grained soils as clays and silts. In sandy soil the water is said to rise not more than two feet.

Soil life has its importance along with air and water. The chief living organisms are bacteria, fungi, and animals. Fungi and bacteria which are usually numerous in the soil are great scavengers. They cause the decay of the dead bodies of animals and plants, or, in other words, the production of humus which is rich in such plant food as soluble nitrates. Bacteria are more numerous near the surface of the soil, becoming fewer at greater depths. They thrive best where there is warmth, moisture, and as a rule oxygen, and, of course, they must have organic food. They do not thrive well in sour soils. In bogs and in other water-soaked soils the absence of air prevents the growth of the proper humus-forming bacteria and the soil becomes sour by the accumulation of acids from the dead vegetation. The organic material, instead of being turned into nitrates, is changed to peat.

The plant cannot use the free nitrogen in the soil air nor certain nitrogenous compounds found in humus, such, for example, as ammonia. In the paragraph dealing with leguminous tubercles, the importance of certain bacteria, nitrogen fixers, is pointed out. There are, however, other bacteria which are important in connection with the supply of nitrogen. These are nitrifying bacteria. One of these (Nitrosomonas) oxidizes ammonia to nitrous acid (HNO_2). Another (Nitrobacter) oxidizes nitrous acid to *nitric* acid (HNO_3). Nitric acid thus produced may combine with other substances in the soil, forming soluble nitrates useful to plants. Comment upon other soil life would take us far beyond the limits of this chapter.

Kinds of Roots.—Based upon the manner of their origin roots are spoken of as *primary*, *secondary*, and *adventitious*. The primary root is the first root originating in the embryo; secondary roots are those which spring from the primary root. Secondary roots may branch repeatedly producing other secondary roots of higher orders of the same system. Adventitious roots arise from other parts of the plant, as stem and leaves. Adventitious roots are common in the cereals. The numerous fine thread-like roots of plants like the grasses are called fibrous roots. Fibrous roots

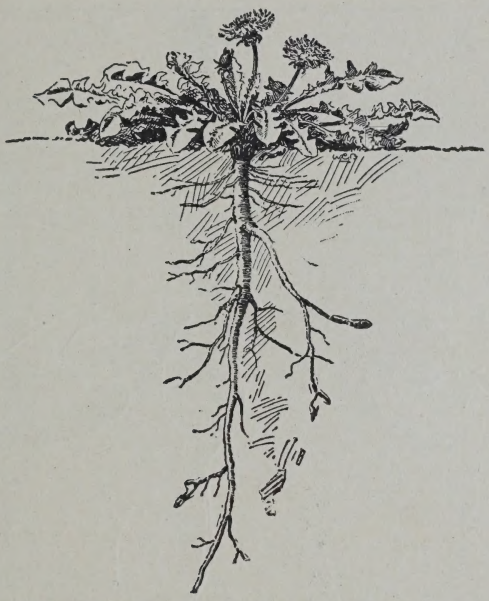


FIG. 144.—A dandelion plant showing its tap root. (From Bailey, "Encyclopedia of Horticulture," Macmillan Co.)

are usually adventitious in origin. The primary roots of corn and the cereals do not become permanent but belong to those referred to as temporary roots.

Modified Roots and Their Special Functions and Adaptations.—Apart from the usual functions of anchorage and the absorption of water and solutes, roots display many additional uses which are associated with specially developed structures and special adaptations.

Roots as Storage Organs.—One of the slightest departures from an ordinary root is found in the *tap root*. This is the primary root which continues growth straight downward, as in the dandelion (Fig. 144). In such roots as the carrot, beet, turnip, and similar biennial and perennial plants, the enlarged tap root is a combination of root and stem, known as a

crown root. Here the internodes are so short that all foliage leaves seem to spring from the broad upper end of the root. These roots are composed chiefly of ground tissue, the vascular tissue being poorly developed. In the beet several separate, and poorly developed rings of vascular bundles are developed in the ground tissue which in appearance suggest annual rings. The zones or rings are not like annual rings of wood since they are not developed from a permanent cambium, but arise in the ground tissue during the short season of development.

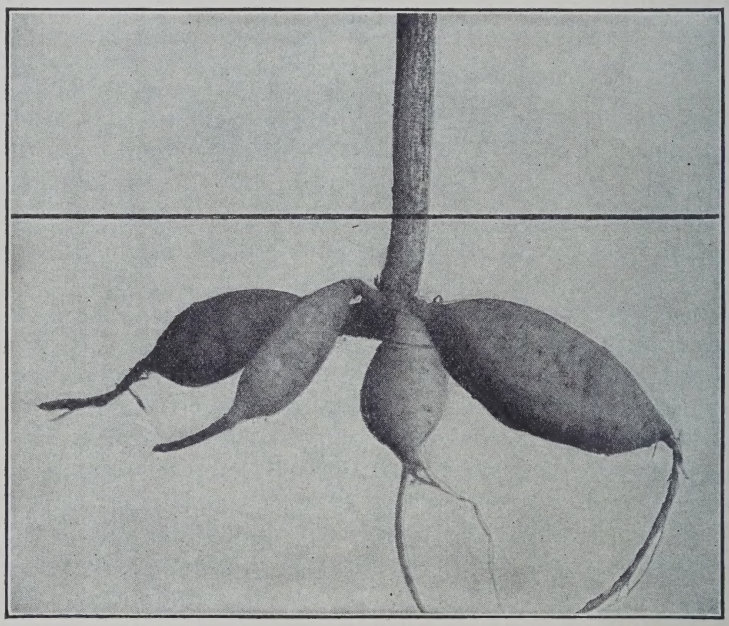


FIG. 145.—Tuberous roots of Dahlia. (Gager.)

Another form of storage root is seen in the thick tuber-like root of the Dahlia, the *tuberous root* (Fig. 145). These roots which spring from the stem are greatly thickened a short distance from their attachment to that organ.

The sweet potato is also a tuberous root, although it is a nearer approach to the crown root than that of the Dahlia.

The food stored is chiefly starch, sugar, and protein. The sugar beet is extremely rich in sugar. Sugar is present in the carrot and sweet potato, although starch is very abundant in the latter, while the root of the Dahlia reveals the carbohydrate, *inulin.*

Roots as Organs of Support.—Roots functioning in this manner fall in two classes, prop, or buttress roots, and clinging roots. *Prop roots* are

developed somewhat above or at the surface of the ground. A familiar example is seen in the stalk of Indian corn with its circles of roots springing just above a few of the lower nodes. Forest trees, like the White Elm and certain trees of the tropical forest, develop broad, and thin, board-like roots near the ground which serve as buttresses.

A peculiar form of supporting root is seen in the *stilt-roots* of the Mangrove and Screw Pine (Pandanus). The mangrove growing in salt marshes appears as if lifted out of the water by means of so many stilts.

One of the most notable cases is the Banyan Tree, in which the adventitious roots arising from the branches, grow vertically downward and

FIG. 146.—A Banyan tree, showing development of numerous prop roots. (Gager.)

become attached to the ground, suggesting so many props (Fig. 146). These prop roots may change into trunks and repeat the process, with the result that in time one tree will give rise to a small forest.

Of clasping or clinging roots, some of our native vines afford excellent illustrations. The older stems of the Virginia creeper (*Psedera quinquefolia*), the poison ivy (*Rhus toxicodendron*) and other clinging vines like the English ivy (*Hedera helix*) and the Boston ivy (*Psedera veitchii*) cling to a wall or other flat surfaces by means of roots. The manner of forming the holdfast is similar to that described for clasping stems.

In the moist tropical forests slender-stemmed plants cling to tree trunks by long roots which pass around the tree like so many tightly bound ropes (Fig. 147).

FIG. 147.—Roots as holdfasts. A scene in a tropical forest. The cord-like roots of this climbing Ficus pass around tree trunks like tightly bound ropes. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

Roots as Aerating Devices.—Certain plants which grow in swamps, or root in the mud under water, develop roots which are thought to form passages for supplying air to the underground parts. The bald cypress (Taxodium) produces tall conical growths, "knees" (pneumatophores)

which extend up through mud and water into the air (Fig. 148). In the bark of the "knees" pores or lenticels are present which may facilitate the supply of air to the roots below.

In the plant, *Jussiaea repens*, a half-floating, marsh plant, some of the roots develop cucumber-shaped structures which rise to the surface and apparently transmit air to the parts under the water (Fig. 149).

FIG. 148.—Aerating Roots, (*Pneumatophores*) of Cypress trees growing in marshy ground which is often flooded. The numerous conical growths, "knees" spring from the roots. The Long Moss hanging from the branches is the epiphyte, Tillandsia, a member of the Pineapple family. (From Schimper's "Plant Geography," The Clarendon Press.)

These peculiar structures are composed of loose open tissue (*aerenchyma*) with large intercellular spaces, which facilitate the passage of air.

Aerial Roots of Epiphytes.—Plants which grow merely attached to other plants without being in any way parasitic, and which have no connection of their own with the ground, are epiphytes. In some tropical epiphytic orchids numerous roots dangle in the air like so many cords (Fig. 150). Those roots have a loose porous cortex which soaks up rain and passes it to the tissue beneath. In the South Atlantic and Gulf States, the epiphyte, Tillandsia, commonly known as "long moss" or

"Spanish moss" is very abundant growing in hanging masses from the branches of the live oak, bald cypress, and other trees (Fig. 148). It is not a moss, however, but a flowering plant belonging to the Pineapple family. The long slender stems and the small narrow leaves, which are clothed with soft hairs, give the masses the appearance of gray Lichens hanging from the branches of the trees. In some plants the aerial roots are flat and green, capable of carrying on photosynthesis.

FIG. 149.—Aerating roots of *Jussiaea repens*, a marsh plant. The tuber-like roots are composed largely of a loose tissue with many intercellular spaces (Aerenchyma), which supply air to parts under water. (From Goebel's "Organophry of Plants," Clarendon Press.)

Water Roots.—Certain small floating aquatic plants, such as duck weeds and the small water fern, Azolla, possess tiny roots which hang downwards in the water. Their tips are covered by large root caps known as *root pockets*.

FIG. 150.—Aerial roots of an epiphytic Orchid. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

Roots Adapted to Unusual Processes of Nutrition.—Roots of certain plants are associated with other organisms in processes of nutrition which

are very unusual. In one category the relation of the two organisms is one of reciprocity or mutual helpfulness (mutual symbiosis) while in another it is true parasitism. The case which is best known and which is of greatest economic importance to man is the association of certain bacteria of the soil with roots of leguminous plants.

Root Tubercles of Leguminous Plants.—The roots of such plants as peas, beans, and clover, are associated with certain bacteria of the soil in a peculiar process of nutrition concerned with securing nitrogen compounds for the plant. Nitrogen compounds, nitrates, are very important food constituents. Although the plant is surrounded on all sides by air extremely rich in free nitrogen (nearly 80% by volume), the plant is unable to utilize the nitrogen of the air; this element must enter through the roots in the form of soluble nitrates, which are in the soil, unless the plant is aided by certain bacteria.

The bacteria (*Bacillus radicicola*) found in the soil enter the roots of leguminous plants, chiefly through the root hairs, and stimulate the roots to form abnormal growths, or *tubercles* (Fig. 151, A). These bacteria are able to assimilate the free nitrogen of the air. In the cells of the tubercles the bacteria live and multiply at first as parasites upon the root cells. By the time the tubercle has reached its definite size, the bacteria have become rich in protoplasm. At this point the roots of the plant begin to digest and assimilate the bacteria, which are rich in nitrogenous material. The bacteria are consequently the intermediary through which the bean or clover secures the important nitrates. The bacteria are often referred to as *nitrogen fixers*.

We have here a coöperation of two different organisms, each contributing to the welfare of the other. In the early growth of the nodule the plant supplies food for the bacteria, while at a later period the bacteria are consumed as food by the plant. The living together of two different organisms in a relation of mutual benefit is known as mutual symbiosis, physiological partnership, or conjoint life.

The effect upon a plant growing in soil containing the tubercle bacteria and upon the same kind of a plant grown in a similar soil but without the tubercle bacteria is well illustrated in Fig. 151, B, C. The plants of the two cultures grew from the same kind of seed, and they are of the same age. The soil of culture B contained no root-tubercle bacteria, while those organisms were present in the soil of culture C.

After such plants as beans, peas, and clover have grown in the soil, the soil is left much richer in nitrates. If such plants are plowed under the soil is greatly enriched by this *green manure*.

Mycorhiza.—The roots of very many plants, notably certain forest trees, such as beech, oak, maple, etc., are enwrapped by the vegetate part

FIG. 151.—Roots and tubercle-forming bacteria. A, root of Windsor bean (*Vicia faba*) thickly beset with tubercles. B, C, two cultures of peas of the same age and from the same kind of seed, one, B, without root-tubercle bacteria and the other, C, with the bacteria in the soil. (A, after Strasburger; B, C, after Frank.)

of certain mushrooms common in soils rich in humus. Such roots are known as mycorhiza, the term really meaning roots infected by fungi.

Two different types of the mycorhiza state are recognized. In one the fungus lives outside the tissue of the plant with which it is associated, *ectotrophic mycorhiza*, and in the other the fungus penetrates the tissue, living between and inside the cells, *endotrophic mycorhiza*.

In external mycorhiza the fungus, consisting of many entangled filaments, a *mycelium*, forms a complete weft-like cover over the entire

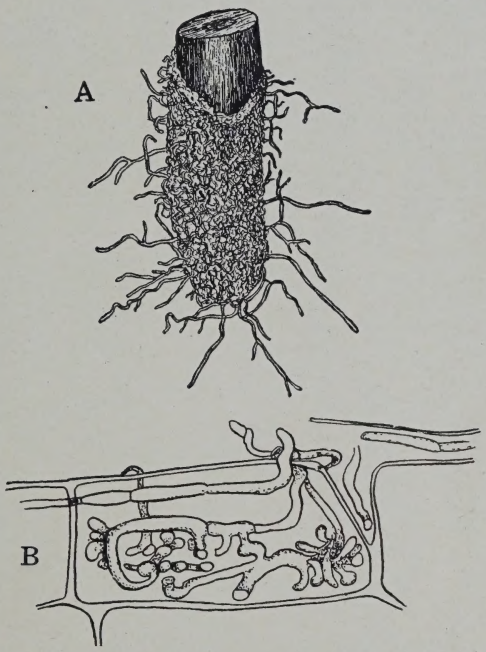


FIG. 152.—A, external (ectotrophic) mycorhiza fungi completely enwrapping the tip of a beech root. B, internal (endotrophic) mycorhiza; a single superficial cell of the young root of the heather (*Calluna vulgaris*), showing the endotrophic fungus and its penetration of the cell wall. (A, after Pfeffer, B, after Rayner.)

tender end of the root (Fig. 152, A). As a result the root-ends are often irregular in form. The fungal filaments do not penetrate the cells of the root but force themselves between the epidermal and cortical cells. The complete functional relation between root and fungus is not satisfactorily understood. There is evidence to show that the fungus absorbs moisture, and perhaps some organic material from the soil, thus to some extent taking the place of the root hairs, while in return the fungus absorbs some food from the root. If this be true the relation of the two organisms is a reciprocity, or one of mutual symbiosis.

One of the most remarkable cases of mutual relationship between a fungus and a flowering plant is exhibited by the Indian Pipe (Monotropa) (Fig. 153). The plant is white in normal color, resembling, when not in bloom, a potato sprout grown in the cellar. Chlorophyll is not developed,

FIG. 153.—The Indian Pipe, or Ghost Plant, Monotropa.

the plant depending upon organic material derived from a fungus which grows in intimate connection with stem-like roots. The fungus absorbs for the Monotropa water, mineral salts, and organic matter set free in the decay of humus; in return the fungus doubtless secures food from Monotropa.

The internal mycorhiza are characteristic for certain orchids, Rhododendron, and heather. In the heather (*Calluna vulgaris*) the fungus is found not only in the root, but in the stem, leaves, flower, and even in the seed coat. The embryo, however, is free from the fungus. Shortly after germination the seedling is infected from the seed coat. This plant seems

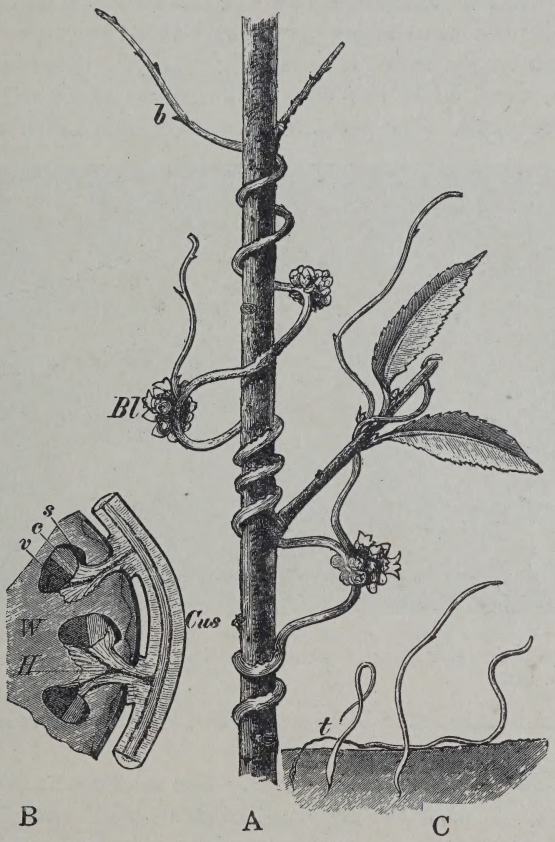


FIG. 154.—The Dodder, a stem-twining parasite. A, branch of willow with parasite twining clockwise around it. *Bl*, flowers; *b*, reduced leaf. B, sector of cross section of host stem (W), showing attachment of parasite, *Cus*, by means of its sucker roots, H. Note that the bast of the sucker root joins the bast of the host, and the wood with the wood of the host. C, seedlings of the parasite rooted in the soil; *t*, seedling with dead root.

to require the fungus for its normal development. In the bird's nest orchid, Neottia, infection is established early in the germination of the seed. The short rhizome develops the crowded fleshly roots that form the so-called "bird's nest" under ground. The nourishment of the plant is saprophytic, through the medium of the fungus. The fungal filaments

are confined to cells of the cortex of the root, but they communicate with the soil by outward-growing filaments.

Parasitic Roots.—Differing from the relation of the two associated plants described in the preceding, is that of true parasitism. Here the roots of the parasite penetrate the tissues of the host, bast joining histologically with bast and wood with wood. A very well known example is the Dodder (*Cuscuta*) whose stem winds about the stem or leaf of its host, the plant upon which it feeds (Fig. 154, A). Like other parasitic seed plants, the Dodder has only rudimentary leaves and it does not develop chlorophyll. The peculiarly sensitive roots which penetrate the

FIG. 155.—*Rafflesia padina*, a flowering plant of Java, parasitic upon the root of a tree. One plant is in full bloom. (From Kerner's "Natural History of Plants," A. Blackie & Son, Ltd.)

tissues of the host, as seen in Fig. 154, B, are called *haustoria*, or *sucker roots*.

The Dodder develops from its seeds. The seedlings at first root in the soil (Fig. 154, C), while slender vine-like stems make sweeping curves in the air. If the stem comes in contact with a suitable host, it will attach itself by means of the sucker roots and all connection with the soil will disappear following the death of the seedling root.

In this connection it is of interest to note the remarkable Javanese parasite, Rafflesia, which grows upon the surface roots of certain trees in Java and Sumatra (Fig. 155). The plant consists of a single gigantic flower, about three feet in diameter, the largest flower known, borne upon a very short stem, whose few haustorial roots penetrate the root of the host.

Native to Indiana and the Middle West are two well known parasites, the Beech Drops, (*Epifagus virginiana*) parasitic upon the roots of beech

trees, and the Squaw Root (*Conopholis americana*), which is parasitic upon roots of oak trees. These plants are colorless when young, turning brown with age. The former has a much branched stem about a foot tall; the latter resembles a colorless asparagus shoot just emerging from the ground. The Mistletoes (Phoradendron and Arceuthobium) which are parasitically rooted to branches of trees are half-parasites owing to the presence of chlorophyll in leaves and stems.

TOPICS FOR REVIEW AND DISCUSSION

How do roots differ from stems?

Is the root system spread out in the soil as regularly and symetrically as the branches of the stem are spread out in the air?

Name some plants whose roots penetrate deeply into the soil and a few shallow-rooted plants.

Why is the growing end of the root smooth and free from root hairs?

As a rule, are root hairs of long or short duration?

Name some plants which possess multicellular root hairs.

Do root hairs develop upon roots of aquatic plants?

How does the origin of root branches differ from that of stem branches?

What constitutes the primordial tissue in the root of the maidenhair fern?

Will roots of a plant penetrate more deeply into the soil in dry seasons than in wet seasons? Why?

Does secondary thickening occur in the roots of any class of plants?

What becomes of the cortex in old roots of dicotylous plants?

Is cork developed in roots? If so, where does the cork cambium originate?

Are the rings seen in a cross section of a beet annual rings?

What is diffusion? Imbibition? Osmosis?

Explain how water and substances dissolved in it pass through a membrane.

Do different substances tend to pass through a membrane independently of each other?

What is meant by osmotic pressure?

What happens when a leaf wilts?

Is the osmotic pressure ever sufficiently great to burst the cells?

What is the difference between a dead membrane and the live plasma membrane as regards osmosis?

What is meant by the selective power of the living membrane?

Is this selective power of any value to the plant?

If a seedling plant be placed with its roots in a 10 per cent. salt solution it will wilt. Why?

Dry commercial fertilizer added to the soil in too large quantities will injure the plant. Why?

What is plasmolysis? How may a cell be plasmolyzed? May the plasmolyzed protoplast be made to return to its former state of turgidity?

What is the humus of the soil and from what is it derived?

Was the soil in your locality derived from the underlying rock, or was it brought there by water or by moving ice (glaciers)?

Distinguish between drained and undrained soil.

What is gravitational water? Capillary water? Hygroscopic water?

Which condition of soil water is not available to plants?

What is the principle of tile drainage? What water is removed by properly laid tile?

What is the water table?

Will water rise higher in a capillary tube than in one of large bore?

Will water rise higher in coarse soil than in finely pulverized soil? In clay soil or in sandy soil? Why?

Which kind of soil will dry out sooner, cloddy or finely pulverized?

What is meant by the expression, "sprinkle the soil with a garden rake"?

Why may plants wilt on being transplanted? Why will shading the plant assist in preventing wilting?

What enables the partly wilted plant to recover?

Which is the best time to transplant, when the ground is dry or following a rain?

Why is it often beneficial to remove a few older leaves before transplanting the plant?

What is soil life? Name several forms of soil life.

What form of soil life do you think is of greatest importance?

What is sour soil? Why does soil become sour?

What did Charles Darwin find out in regard to soil and earthworms (angle worms, fishing worms)?

What do earthworms eat?

Are earthworms beneficial to the soil?

Would a number of earthworms in the soil of a potted plant injure the plant any? Why? How would you get rid of such worms?

What are *nitrifying* bacteria?

What parts of the plant take nitrates and other soluble salts from the soil? How is the nitrogen and other substances returned to the soil?

What are modified or metamorphosed roots?

List all the kinds of modified roots mentioned in the text.

Distinguish between a tuberous root and a stem tuber.

Is it botanically correct to speak of a Dahlia bulb?

Name some roots rich in starch. Some rich in sugar.

What are cypress "knees"?

Name some plants which possess aerial roots?

Is the so-called "long moss" or "Spanish moss" really moss?

What are the root tubercles of leguminous plants? How are they formed? What is mutual symbiosis?

What constitutes green manure?

What are mycorhiza?

Name two plants which possess mycorhiza.

What is the "bird's nest" orchid?

How do parasitic roots differ from ordinary roots? Name three parasitic flowering plants native to the United States.

Explain the relation of a parasitic root to the tissue of the host plant.

The dodder (Cuscuta) starts from a seed in the soil. How does it become attached to the host? What becomes of its soil root?

What flowering plant is referred to as a half-parasite? Why?

What is Rafflesia? Where is it native?

Why will some fleshy fruits split open in a wet season?

Why is iodine more abundant in the tissues of certain brown seaweeds than in sea water?

Explain how dry seeds take up water.

CHAPTER VI

MOVEMENT OF WATER AND FOOD IN PLANTS

Without water, life processes in plants are impossible. The amount of water in individuals manifesting life varies from that of a relatively small quantity in seeds and certain dormant vegetative tissues to that totalling 95% to 98% by weight in certain fungi. To be sure, spores, seeds, and certain vegetative parts in the dormant condition may remain alive,—they are viable; but the life processes in those structures are such that they cannot be readily demonstrated or measured by ordinary means. In the dried state those structures manifest passive life only, although all conditions necessary for the manifestations of active life may be present, except a sufficient quantity of water.

In submerged aquatic plants, in which all parts are in direct contact with water, the problem of transportation is relatively simple. The same may be said of land plants of small proportions. In regard to large plants, however, living in the air of ordinary humidity and attached to the soil, the problem is different. In the case of tall trees, water is taken in at one set of extremities, the roots, and then transported to the other set of extremities bearing the leaves, which are far removed from the source of intake. Not only must a large volume of water, with its solutes, be transported to those regions in which rapid growth is taking place, and in which food is being made, but the almost unbelievable quantity lost by evaporation from the leaves and all other tender parts in contact with the air must be replaced.

The Conduction of Water.—The water given off by the plant by transpiration or by exudation was taken up by absorbing organs and then transported to the evaporating surfaces or to the organs of exudation. In the lower plants, or in those of small size and simple structure, osmosis and diffusion from cell to cell may suffice for adequate transportation. But in the higher plants other processes and a special conducting system are involved. In a foregoing chapter it was pointed out that the vascular tissue functions as the system of rapid transit for the conduction of liquids. The root hairs absorb water and mineral salts from the soil, and by diffusion and osmosis, this water is conveyed from cell to cell of the cortex of the root to the xylem of the vascular bundles, through which a continuous stream is rapidly transported to the most remote extremities of stems and leaves.

Rôle of the Xylem.—That part of the vascular bundle which transports water and dissolved substances from roots into the plant is the xylem, and this fact is easily demonstrated. We usually think of the xylem as conducting the water upward in the plant, or from base to tip, but the direction may be readily reversed. If a branch be removed from a suitable woody plant and supported with the cut-off tip end in water, it will be seen that the water now moves in the reverse direction, i.e., from tip to base. If the stem be girdled, and colored water, such as a dilute solution of eosin, be used, it will be observed that the water does not pass through the bark, which contains the phloem of the vascular bundles. The xylem transports not merely water and dissolved salts, but digested food as well. Chemical analysis has shown that the vessels of the xylem, especially in the spring, may contain sugar, protein, and amides (nitrogenous food of simpler composition than proteins). At other times of the year these compounds are present, but in smaller quantities. Notable examples are the maples and birches.

Function of the Phloem.—It is very evident that in many plants the bulk of the plastic food is made in parts of the plant that are remote from the parts in which the food is used or stored. The surplus food made in the leaves and other green parts is transported to regions of growth and storage, and stored food, in turn, must be transported from the storage organs to the growing tissues.

If a tree trunk be girdled by the removal of a ring of bark the tree will die at the end of the season or soon thereafter, if new bast be not formed. Water passes up to the leaves, but food made by the leaves, which is necessary to nourish the living parts of the roots, is cut off and the roots are starved. For the same reason the bast below the girdled zone of a branch of a tree may shrivel and die, while that above will continue to live and grow.

It can be shown that the elements of the phloem, especially the sieve-tubes, contain, along with other substances, carbohydrates, proteins, and amides, in large quantities; and it is easily demonstrated that these substances are conducted upwards or downwards in the stem by the phloem. For example, a willow cutting is girdled by the removal of a ring of bark a short distance from its lower end, and supported in an upright position with its lower end in water (Fig. 156). In due time the cutting will send out roots and shoots. From the part of the stem below the girdle the development of roots especially will be much less extensive than above the girdle. Moreover, no food will be stored in the bast or cortex below the girdle.

The sieve-tubes are well adapted to the conduction of proteins and other colloids, which diffuse throughout the cell and through the cell

walls with difficulty. The office of the companion cells is not so well understood. They may take over materials from the sieve-tubes and pass them on to other structural elements for immediate use or storage. It is not improbable that companion cells may also act as glands to change substances in the sieve-tubes, or after they are taken over to be passed on. The phloem parenchyma seems to be well fitted to conduct carbohydrates and amino compounds in a longitudinal direction and turn them over to the vascular rays for storage and for transportation in a radial direction in the stem. The phloem parenchyma, and the parts of the vascular ray most resembling phloem, are the principal places of the storage of protein during the dormant periods of winter and dry seasons.

We may sum up the functions of wood and bast by saying that the wood transports water with dissolved salts and food throughout the plant, while the phloem conducts digested food from places of manufacture to places of use or storage. Food may also be stored in both wood and bast.

The Ascent of Sap in Tall Plants.—Attention has been called to the necessity of the transportation of water and solutes from the young ends of the roots to the most remote extremities of the branches and leaves, a distance of 95 or 100 meters (311 to 328 feet) or more in the case of the tall Sequoia and of the Eucalyptus. The question of what causes the ascent of sap in tall trees still awaits a complete answer. Of the facts, however, which have been well established, certain ones stand out prominently. One is that the roots force or push water into the stem and the other is that the leaves pull water up through the stem.

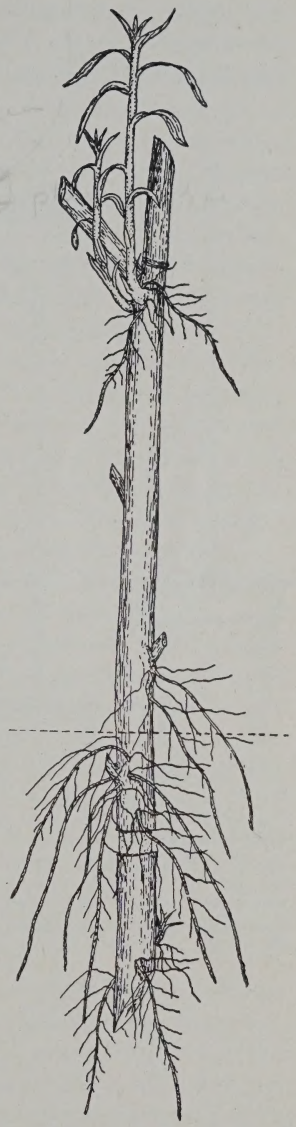


FIG. 156.—Roots and branches developed by a girdled stem of the willow. The cutting was kept in water up to the dotted line.

From the time the seedling emerges from the soil until the death of the plant, an unbroken column of water is maintained in the xylem by the osmotic action of the roots, and it moves upwards from the

absorbing ends of the roots to the leaves where water is being given off continually by transpiration. This column of water is known as the *transpiration stream.* During the winter, when the plant is dormant, very little water is transported in comparison with that given off during full foliage of spring and summer.

FIG. 157.—Root pressure. A glass tube has been substituted for the stem of the plant, and water has risen some distance in the tube.

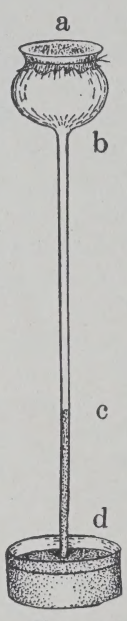


FIG. 158. Apparatus to show suction caused by evaporation of water through a membrane. *a*, membrane; *b*, thistle tube; *c*, height to which mercury has risen; *d*, dish of mercury.

Root Pressure.—As already stated the water absorbed by the root hairs passes by means of osmosis from cell to cell in the cortex to the vascular cylinder where it rapidly ascends. That water is forced into the stem by the osmotic action of the roots, may be shown by a simple experiment. The stem of the Dahlia, or other suitable plant, is cut off a few inches above the ground, and, by means of a short piece of rubber tubing, a glass tube of small bore is attached water tight to the end of the stem connected with the roots, as shown in Fig. 157. In a few hours, water forced out with considerable pressure through the end of the stem will rise in the glass tube, and continue to do so for a few days. The phenomenon is known as *root pressure.*

When grape vines are pruned a little too late in the spring, water will drop in considerable quantities from the cut ends. The water comes from the vessels, and it is forced out by root pressure. The flow of sap when a sugar maple tree is tapped in late winter or early spring is due, in a large measure, to root pressure. The outflowing sap contains mineral salts, and large quantities of organic substances. The sap of the sugar maple (*Acer saccharum*) contains about 3% of common sugar.

The Lifting Power of Transpiration.—That transpiration from the leaves creates a suction, or lifting power, which tends to stretch or pull the column of water in the xylem, may also be demonstrated experimentally. A thistle tube with the large end closed by a membrane, such as a piece of prepared bladder, is completely filled with water, and supported in a vertical position with the open end of the tube in a dish of mercury

(Fig. 158). After a time the mercury will have risen in the tube. Water passes out of the tube by evaporation from the surface of the membrane, and mercury rises in the lower end of the tube to take the place of the evaporated water. The mercury is forced into the tube by the pressure of the air. The evaporation from the surface of the membrane brings about a suction, or lifting power, in the same manner as transpiration from leaves tends to stretch the column of water in the xylem. It must be borne in mind that this simple experiment does not show, and it is not intended to show, the cohesive strength of liquid water. It shows that evaporation can produce a lifting power, or suction. Suitable experiments, however, have shown that the cohesion of liquid water is a very important factor in the movement of the transpiration stream.

It can be shown experimentally that, during active transpiration especially, the water and bubbles of gas in the vessels of the xylem are under tension; the transporting stream is being stretched. If one cuts in two, under mercury, the stem or branch of a rapidly transpiring plant, it will be found that the mercury is sucked rapidly into the vessels from the cut surface. The phenomenon is referred to as *negative gas pressure*, and it is most pronounced on warm, sunny days which favor transpiration.

Of the two forces, root pressure and transpiration pull, the latter is doubtless the more effective. As has been shown water will rise in a stem when severed from the root. At certain times, especially when much water is being evaporated from the leaves, root pressure is scarcely to be detected, and it seems that there is none. This is probably due to the fact that the pull of transpiration is so much greater than root push that the latter seems absent. It is equally true also that the action of the roots continually supplies the water and gives the current a start.

By way of summary, it may be stated that the underlying causes of the movement of water in the stems of plants are transpiration from the leaves, imbibition of cell walls, cohesion of liquid water, and root pressure. Other forces such as capillarity, imbibition and atmospheric pressure are operative.

In discussions of the movement of water, root pressure is doubtless underestimated, owing to the fact that it is not apparent when transpiration is active. An automobile with just enough gas supplied to idle the engine in going down grade will, by its momentum, push harder than the engine is pulling, but that does not prove that the engine does not pull at all.

TOPICS FOR REVIEW AND DISCUSSION

What per cent. of the weight of green wood is water? Of lettuce leaves? Of mushrooms?

Distinguish between active life and passive life.

Where does the water which evaporates from the leaves enter the plant?

How do water and solutes which are absorbed from the soil find their way to the xylem of the vascular bundles?

The cells of the protoxylem are devoid of living contents. How does the water pass from the living cells of the cortex into the xylem cells?

What is transported by the xylem? By the phloem?

When a sugar tree is tapped for sugar water does the sap come from the wood or from the bark? How deep is the hole made in the processes of tapping?

Why will not sugar water run from a tapped tree after the buds begin to swell, and later?

How did the sugar come to be in the wood?

Enumerate all the forces which you think operate in the ascent of sap in tall trees (over 40 feet).

What is the role of the leaves in the ascent of sap? Of the roots?

Does the sap ascend in the sap wood or in the heart wood? Why?

What is root pressure?

What is negative gas pressure?

In seasons of drought why may the twigs of the tree farthest from the roots be among the first to suffer?

Do you think there is a limit to the height which may be attained by a tree?

What part of each annual ring transports the greater part of the sap?

CHAPTER VII

SEEDS AND SEEDLINGS

A seed consists of an embryo plant provided with stored food and surrounded by a cover, the *seed coat*. The food is stored in either the embryo or in a tissue, the *endosperm* which surrounds the embryo. If all

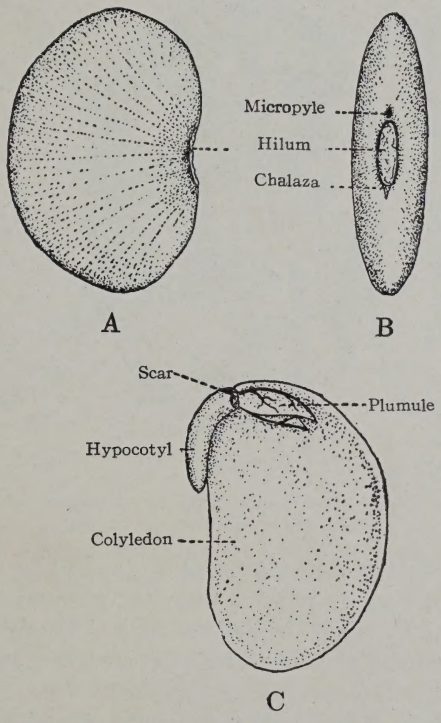


FIG. 159.—Seeds of Lima bean soaked in water. A, side view; B, view from the concave edge; C, embryo with one cotyledon removed, showing cotyledon, hypocotyl (sometimes called radicle), and scar remaining after removal of cotyledon.

the food be stored in the embryo, as in the lima bean, no endosperm is present in the mature seed.

Seeds Lacking Endosperm at Maturity.—As a representative of this type of seed we may select the familiar Lima bean (*Phaseolus lunatus*).

Viewing the seed externally, we observe at the concave edge a large scar, the *hilum*, indicating the place at which the seed was attached by a short stalk or cord, the funiculus, to the pod, or fruit (Fig. 159, A, B). Near the hilum is the *micropyle*, an opening in the seed coat. The seed coat is a skin-like cover consisting of two layers. In some seeds the coat consists of but one layer.

The embryo has a rather stout stem, the *hypocotyl*, to which is attached at its upper end two large opposite cotyledons (*C*), one being shown in the figure.

The part of the stem above the cotyledons is the epicotyl which bears the first two foliage leaves in a young stage of development. Between

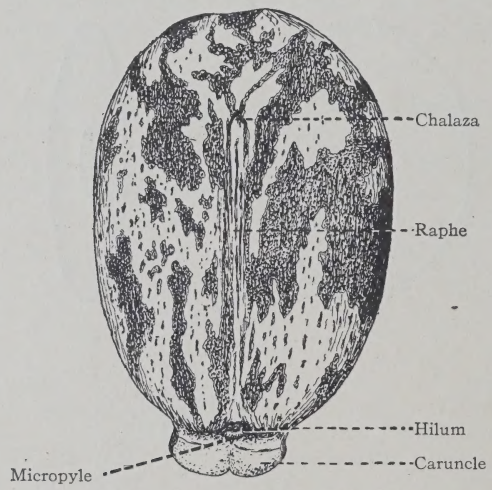


FIG. 160.—Castor-oil seed (*Ricinus*) seen from the flattened side, showing caruncle, hilum, raphe, chalaza, micropyle.

these two leaves is the primordium of a bud. The epicotyl with its young leaves has long been referred to as the *plumule*. The lower, free, rounded end of the hypocotyl is the beginning of the primary root.

Seeds with Endosperm.—In this type of seed, the embryo is relatively small in comparison with the bulk of the seed.

A good example is the seed of the castor-oil plant (*Ricinus communis*). Here the seed coat develops into a rather firm, brittle shell, *testa*, often revealing conspicuous patterns (Fig. 160). At the micropylar end of the seed there is developed from the seed coat a conspicuous mass of tissue, the *aril*, known also as the caruncle. The micropyle is located at the posterior edge of the aril on the flattened side of the seed (Fig. 160).

The embryo has a short hypocotyl, bearing at its upper end two opposite, broad but very thin cotyledons. Fig. 161, A, is a view of the seed

cut in two flatwise, showing the surface of one cotyle lon and the hypocotyl. Between the cotyledons is the primordium of a bud. Surrounding the embryo is the massive endosperm, rich in oil and protein. In Fig. 161, B, which represents the seed cut in two longitudinally at right angles to the surface of the cotyledons, the relative size of embryo and endosperm is shown. In this and in similar seeds the cotyledons digest and absorb the endosperm during germination, and function also as the first foliage leaves after germination.

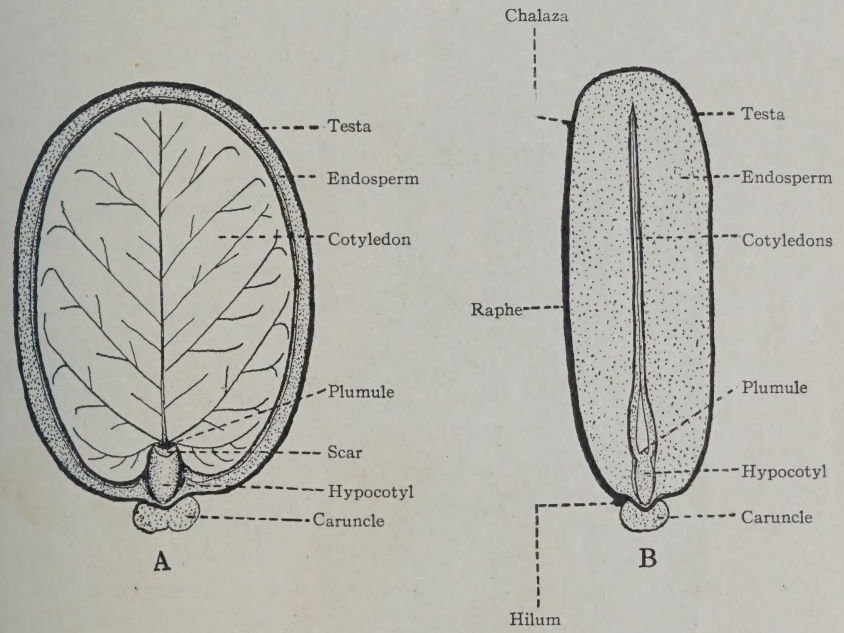


FIG. 161.—Castor-oil seed (*Ricinus*). A, view of seed halved flatwise, showing surface of cotyledon and hypocotyl. B, longitudinal section at right angles to the surface of the cotyledons.

The Aril.—The term, *aril*, is applied to any special fleshy or succulent outgrowth of the funiculus or of the seed coat. Among the common wild plants whose seeds possess conspicuous arils are the twin leaf (*Jeffersonia diphylla*) and the Celandine poppy, (*Stylophorum diphyllum*). The caruncle of the castor-oil seed has already been mentioned. The large succulent aril covering the seed of the nutmeg constitutes mace. Sometimes the term aril is used in a very broad sense to include the hair-like outgrowths of the cotton seed, which constitute the cotton of commerce. The red, juicy tissue developing as a cup about the seed of the Yew tree (*Taxus baccata*) is referred to as an aril.

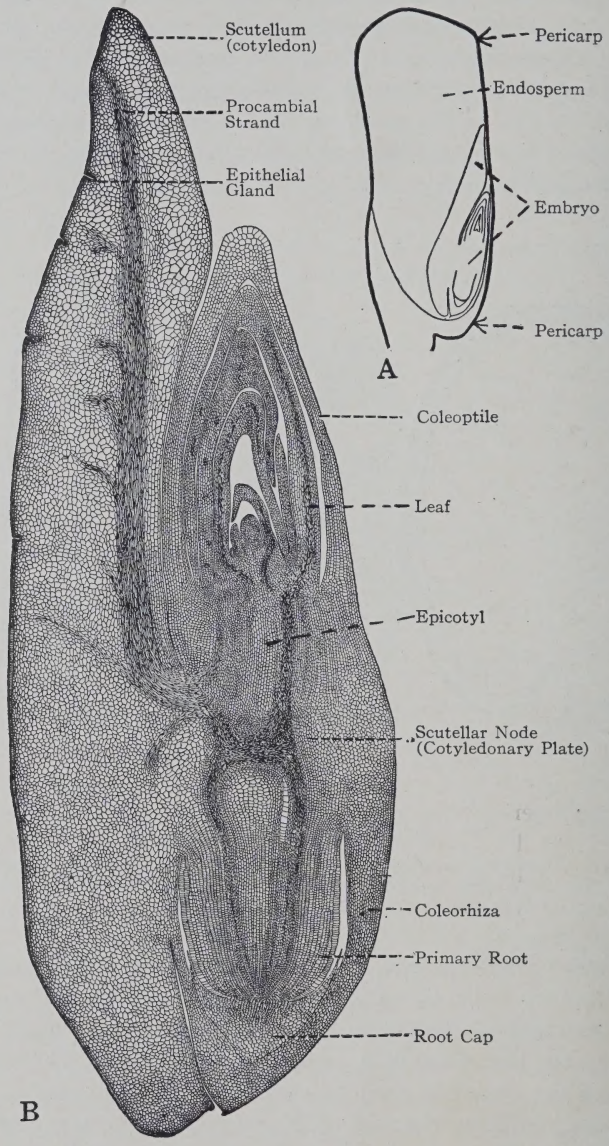


FIG. 162.—A, outline of longitudinal section of a grain of corn at right angles to the flat surface. B, median longitudinal section of the embryo. (After Avery.)

The Seed of the Grass, Indian Corn.—As another illustration of a seed with endosperm at maturity, we shall select the grain of Indian corn. The grain of corn is a whole achene-like fruit called a *caryopsis*. As the grain matures, the wall of the ovulary and the coat of the young seed become grown together and mature as a thin skin-like layer. In a longitudinal vertical section of a grain, the relation of all parts may be easily made out (Fig. 162, A). The embryo is situated at the side, which is marked externally by an elongated depression. The remainder of the seed is the endosperm. The embryo possesses one large cotyledon whose infolded upper margins almost or quite enclose the epicotyl and whose lower portion partly surrounds the hypocotyl (Fig. 162, B). The hypocotyl is covered by the root sheath, the *coleorhiza*. The plumule consists of two or more small leaves, the older folded about the next younger.

The axis of the corn embryo includes the first two or three nodes of the plant. To the first node is attached the cotyledon.

Germination of the Seed.—One of the most fundamental characteristics of most seed-bearing plants, is the fact that the embryo is capable of retaining its viability for a long period of time under a wide range of conditions of moisture and temperature. This property of the seed has undoubtedly played a large role in enabling seed plants to acquire and maintain dominance upon the land areas of the earth. The range of viability in length of time varies from several months or a year to many years. Seeds of the tobacco plant are said to retain viability for about twenty years. Seeds of many Leguminosae also remain viable for a long time (87 yrs.). The story of viable seeds of wheat (mummy wheat) found in connection with Egyptian mummies is without scientific foundation. As a rule the seeds of cereals are comparatively short-lived.

If the proper conditions of air, warmth and moisture are present, viable seeds will germinate, some as soon as they are mature, as in the wheat, or even before they are mature, as in certain varieties of Indian corn, others only after a shorter or longer period of dormancy. During germination the growing embryo has not only the task of digesting the food supplied in the cotyledons or in the endosperm, but it must also free itself from the seed coat and emerge from a cover of soil, both processes being accomplished at the expenditure of much energy, and often involving a severe struggle. It sometimes happens that the embryo of certain seeds becomes severely mutilated in freeing itself from the seed coat.

The first step in germination is the imbibition of water. As a result, the embryo and the endosperm, if the latter be present, swell sufficiently to burst the seed coat. In case the seed coat does not burst, as in the seed of the coconut, parts of the embryo force themselves through an opening by the gradual process of elongation.

The expansive force generated by imbibition is often very considerable, as may be realized by filling a thin-walled glass bottle with dry peas, then pouring in water and closing with a stopper. In due time the swelling of the peas may shatter the bottle.

Because of the supply of stored food, germinating seeds are able to generate much energy through digestion and respiration, and they are favorable objects for the experimental demonstrations of the liberation of energy and the processes involved.

As germination progresses, the hypocotyl is usually the first to elongate in dicotylous plants and emerge from the seed coat. It grows, bending

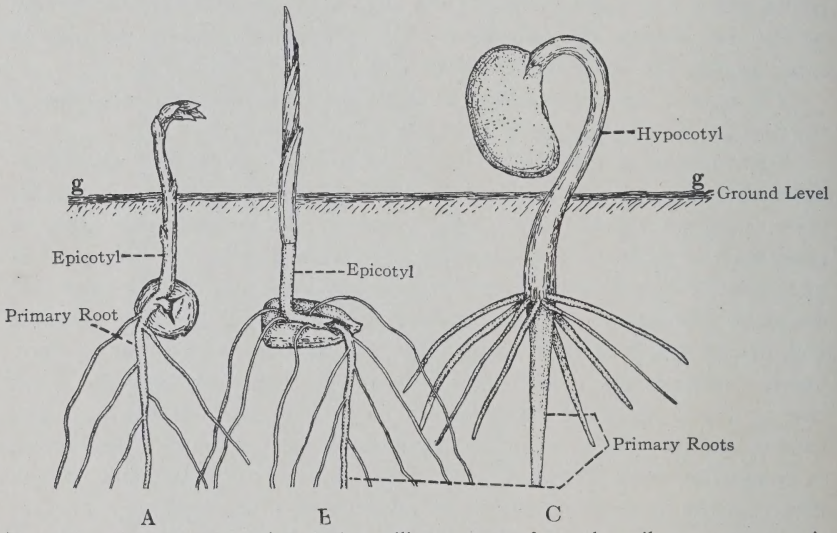


FIG. 163.—Different ways in which seedlings emerge from the soil, or come up. A, garden pea; B, corn; C, Lima bean; g, ground level.

if necessary, straightway toward the center of the earth, and penetrates the soil. The primary root continues growth in the soil, soon developing secondary roots. In seeds like the Lima bean, the cotyledons and epicotyl are lifted above the soil by the elongation of the hypocotyl which makes a crook, thus pulling the bulky cotyledons out of the ground instead of pushing them in advance (Fig. 163, C). In seeds like the pea and Indian corn in which the cotyledon or cotyledons do not leave the seed coat, but remain under ground, the aerial parts are brought above the surface of the soil by the elongation of the epicotyl, or by a number of the internodes above it (Fig. 163, A, B). In the grasses, such as Indian corn, wheat, oats, etc., the outermost leaf of the plumule, which enwraps the younger leaves within, remains closed and elongates until the surface of the soil is reached, then it opens, permitting the other blades to unfold. In the

squash and pumpkin seeds, a peg-like outgrowth of the hypocotyl assists the embryo to free the cotyledons from the seed coat (Fig. 164).

In the meantime, digestion and assimilation of stored food continues, and when about all the food primarily stored in the seed is consumed and the seedling plant is able to shift for itself, germination may be said to be completed.

As stated, seeds of certain plants will not germinate as soon as they are mature, but require a period of dormancy extending over a year or longer. The seeds of the slippery elm, for example, do not germinate until the second year after maturity. During the period of dormancy

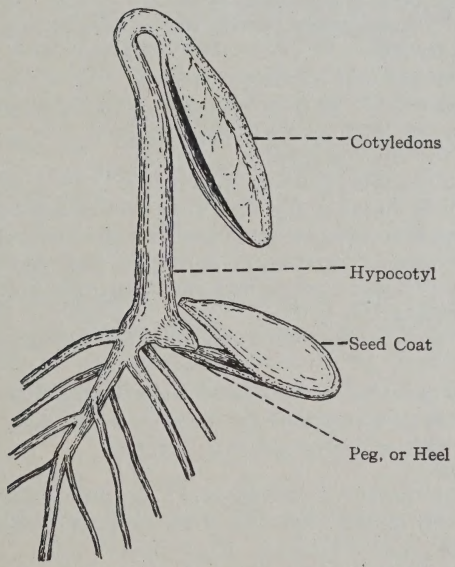


FIG. 164.—Seedling of squash, showing the "peg" or "heel" holding down the seed coat.

certain chemical and histological changes take place which are usually referred to collectively as *after ripening*.

Delayed germination may be due not so much to the need of after ripening as to the hardness and poor permeability of the seed cover. Nursery men and gardeners have long followed the custom of opening such seeds as those of the Canna with a file or by breaking the stony shell of the peach with a hammer.

TOPICS FOR REVIEW AND DISCUSSION

What three important conditions are necessary for the germination of seeds? How would you demonstrate the necessity of each of the three conditions?

Do the embryos of seeds ever experience any difficulty in getting out of the seed coat?

What are some advantages of a hard seed coat? What are some disadvantages?

What is meant by the after ripening of seeds?

How long have seeds been known to retain viability?

What is done to facilitate the germination of seeds with hard seed coats, such as those of Canna, and of the Linden tree?

What may be done to facilitate the germination of the seed of the date palm?

How many "eyes" has the coconut. How many are open?

Is the "flesh" of the coconut embryo or endosperm?

Botanically speaking what is the milk of the coconut?

Are the cotyledons a part of the embryo?

When may the germination of a seed said to be complete?

In a germinating seed what force is most powerful in breaking the seed coat?

What changes take place in a germinating seed?

When seedlings of the garden pea (Pisum) emerge from the soil, why do the cotyledons remain under ground?

Why do the cotyledons of the Lima bean "come up"?

Why does the hypocotyl of the Lima bean crook when the seedling comes up?

What is the "peg" or "heel" of the pumpkin seedling?

What is mace in the botanical sense?

From what part of the plant is nutmeg derived?

What is the aril? Is the aril of any value in the economy of the plant?

What do you think is the function of the caruncle of the castor oil seed?

Have the color patterns on the surface of the castor oil seed any significance?

Do seeds without endosperm possess any advantage over those with endosperm? Which kind will germinate more quickly?

Do you know of any seeds that will germinate before they are completely ripe on the plant?

Would the wheat plant be more valuable to the farmer if the seeds would not germinate for two or three months after the harvest?

Do small seeds possess any advantage over large seeds?

What is a caryopsis?

How many parts are present in the embryo of a ripe grain of Indian corn?

Do you know of any seeds in which the embryo is undifferentiated at the time of maturity of the seed?

Does any other part of the plant than its seeds supply a greater quantity of food for animals including man?

What seeds used as food by man are richest in protein? In starch? In oil?

In your judgment are seeds more efficient objects of propagation than spores?

Did spore-bearing plants appear in the history of the Earth before seed-bearing plants?

Save in a few cases, why must plants bear spores before they can bear seeds?

CHAPTER VIII

UTILIZATION OF FOOD—ENERGY RELEASE

In the preceding chapter we dealt with the processes which have to do with the building up of food from simple into complex compounds, or the storing of energy. We may now consider some of those activities of the plant concerned in the using of food, or the liberation of energy, by which complex compounds are broken up into simpler compounds. The processes involved in the utilization of food may be included in two categories, *digestion* and *respiration*. In these processes there may be brought into play in the plant certain invisible organic bodies, the *enzymes*, bodies which can do the same work outside of the plant as within the cells by which they are produced. Simple experiments will indicate the way in which enzymes work and what they do.

The Work of Enzymes.—If some barley malt be ground to a fine powder, the cell organization will be completely destroyed. The protoplasm will be dead, but from the dead protoplasm there may be separated, by a chemical process, an invisible substance which enables the plant to do a kind of work that cannot be done otherwise under conditions in which cells remain alive. The substance in question, which can be separated from the malt is known as *diastase*. Diastase is capable of doing the same kind of work when separated from the protoplasm as in the living cell. If a small bit of malt diastase be added to some very dilute starch paste in a test tube and kept in a warm place, after some hours no starch will be found in the tube. Another tube of dilute starch paste is kept under the same external conditions, but without the addition of malt diastase. In this tube at the end of the same time as much starch will be present as at the beginning of the experiment, as may be shown by the iodine test. The contents of the tube to which the diastase was added is now boiled after the addition of some Fehling's solution. The result indicates the presence of sugar. Since no sugar was introduced with the diastase, it is clear that starch was changed to sugar; in other words, the starch was digested. The change of starch to sugar may be expressed chemically by the equation: $C_6H_{10}O_5 + H_2O +$ energy of diastase $= C_6H_{12}O_6$. This means that a molecule of starch combined chemically with a molecule of water to make a molecule of sugar, and that the diastase helped to bring about the chemical change. The process which

took place with the aid of diastase changed the starch, a solid, into a solution of sugar. A new compound was formed, and, at the same time, the new compound was left in solution. Diastase belongs to that class of enzymes which bring substances in solution; they are liquefying enzymes.

The killing of the barley plant to make malt, and the processes necessary to separate the diastase from the dead cells, did not destroy the activity of the diastase. If, however, the diastase be treated with a strong acid or alkali, or heated to the boiling point of water, it would then have no effect in assisting the change of starch to sugar. Its action would have been completely destroyed.

Malt diastase is but one of the many substances produced in the living plant cells which assist in bringing about chemical changes. These substances are known as *enzymes*, and their names end in *-ase*. Each enzyme is able to do some specific thing. For example, *invertase* helps to change cane sugar to glucose and levulose; *zymase*, of the common yeast plant, brings about the conversion of glucose to alcohol and carbon dioxide; *lipases* act on oils and fats; *oxidases* facilitate oxidation; *protease* acts upon protein substances, etc.

A few additional examples will serve to illustrate further the character of enzymatic action. When cultivated yeast (*Saccharomyces cerevisiae*) is permitted to grow in the presence of sugar the process of alcoholic fermentation will take place. The yeast, while feeding on the sugar, secretes an enzyme, *zymase*, which assists in a chemical change resulting in the production of two by-products, *alcohol* and *carbon dioxide*, the latter being given off as a gas. During the process heat is also evolved. Some of the energy liberated here results in the production of heat. The following equation will indicate what takes place chemically: $C_6H_{12}O_6$ by action of zymase = $2C_2H_5OH$ (alcohol) + CO_2. If, however, the yeast be supplied with cane sugar instead of glucose, the cane sugar is first changed into more simple sugars. The yeast produces *invertase*, which assists in the chemical change expressed thus:*

$$\underset{\text{cane sugar}}{C_{12}H_{22}O_{11}} + H_2O \text{ by action of invertase} = \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{fructose}}{C_6H_{12}O_6}.$$

Another kind of fermentation takes place following alcoholic fermentation in the complete process of making vinegar from apple cider. Through the growth of yeast the sugar in the cider is changed to alcohol. With the accumulation of alcohol and the lack of sugar, the yeast cells become inactive. Upon this alcohol, some acetic acid bacterium, such as *Bacterium aceti*, feeds, and one of the results is the production of acetic acid from alcohol, as expressed in the equation: C_2H_6O (alcohol) + O_2 by the

* Glucose and fructose differ in that the former rotates polarized light to the right, right-handed sugar, and the latter rotates polarized light to the left, left-handed sugar.

activity of *Bacterium aceti* = $C_2H_4O_2$ (acetic acid) + H_2O. This process is acetic fermentation. From the foregoing, it is seen that acetic fermentation is an oxidizing process, inasmuch as oxygen is utilized, the molecule of alcohol being oxidized to a molecule of acetic acid. The enzyme formed by *B. aceti* is an *oxidase*. The bacteria with the aid of its enzyme changed the alcohol into acetic acid. In the process oxygen was utilized. Oxidation consequently took place, and the enzyme concerned belongs to the class of oxidizing enzymes. There are many kinds of enzymes, and each kind is able to do only its specific kind of work.

Among the many processes of everyday life brought about in part by the action of enzymes are the souring of milk, the conversion of cabbage into kraut, the conversion of green fodder in the silo to ensilage, etc. In the making of bread in which yeast is used, the bubbles of CO_2 liberated by the activity of the yeast converts the more compact and sticky dough into a porous mass, i.e., the dough is made to rise.

It is now apparent from what has been said and from the chemical actions indicated in the foregoing equations, that enzymes are merely helpers. They assist chemical action, but they do not enter into the composition of the substances they help to produce.

Generally speaking, let us say that enzymes are organic bodies produced in the cell, which assist in bringing about chemical changes without entering into the make-up of the compounds formed. Enzymes cannot be observed with the microscope. They are organic bodies, mostly colloidal in character, which can be precipitated by alcohol, preserved dry or in a moist condition by the use of dilute chloroform or other chemicals which prevent bacterial or fungal growth without injury to the enzymes. The action of enzymes is specific; that is, any given enzyme is capable of only one kind of activity. Enzymes are frequently referred to by group names which signify the general result, such as hydrolizing enzymes, which bring substances into solution, as the digestion of starch, and the liquefying of cell walls. Those producing oxidation are oxidizing enzymes, etc.

The activity of many enzymes, such as those producing fermentation, changes complex bodies into simpler ones, and this usually results in the liberation of energy. The energy liberated is manifested in the form of heat, in work done by the plant, and in many other ways that cannot always be readily observed or accurately measured. Enzymes that convert complex compounds into simpler ones are probably best understood. But processes that built up complex compounds, by which energy is stored, go on side by side in the cell with those that liberate energy. The glycerine used in the synthesis of oils and fats mentioned in a preceding paragraph (p. 54) was produced by the breaking up of more complex bodies. Inas-

much as there are enzymes of analysis, there are probably enzymes of synthesis also.

Up to the present time no enzyme is known to operate in phytosynthesis,* the source of energy here being light. In other synthetic processes, however, the energy required may be supplied in part by enzymes. In all cases of enzymatic action, it is not known whether the enzyme is the *source* of the energy or merely the *vehicle* of the energy.

Of the very many enzymes known to science, a number like diastase can be isolated and made available in commercial form.

Respiration.—Respiration should never be confused with breathing. *Plants do not breathe.* Breathing is a term applied to the gaseous exchange in the lungs of an animal. It is purely mechanical and analogous to ventilation, i.e., the taking in of air richer in oxygen and the expulsion of air richer in carbon dioxide. Respiration is the result of chemical processes.

It may be remarked here that in photosynthesis and respiration the exchange of gases is just the reverse. In photosynthesis the intake is carbon dioxide and the output oxygen, while in respiration the intake is oxygen and the output carbon dioxide. The results of the two great processes is also the reverse. Photosynthesis stores energy; respiration liberates energy.

In a preceding paragraph referring to the process of fermentation by the yeast plant, we learned that the yeast grew, feeding upon sugar, and that two by-products resulted, alcohol and carbon dioxide. The alcohol remained in the water containing the yeast, and the carbon dioxide escaped into the air as bubbles of gas. A complex compound, sugar, was broken up into simpler compounds. Another important thing occurred: heat was evolved and set free. Heat is energy, and the energy in this case was produced by the living plant, the yeast plant. Whenever plants use food or break up complex organic compounds energy in some form is set free. We are dealing then with the processes which break up compounds and release energy known as *katabolism.* These processes are just the opposite of those by which food was built up and energy stored, *anabolism.* All of these processes are chemical processes and are known collectively as *metabolism.* Now we may say that those processes, *taking place in the living organism, which liberate energy constitute respiration.*

The yeast plant teaches us another thing in regard to respiration. Yeast will grow in the absence of air. Energy will be liberated without the oxygen of the air, i.e., without molecular oxygen. The oxygen given off in the carbon dioxide (CO_2) was derived from the broken molecules of

* There is some evidence which suggests that there may be some enzymatic action in photosynthesis, or something similar to enzymatic action.

sugar and not from the air. Respiration can take place, therefore, in the absence of air. This is known as *anaerobic*, or *intramolecular* respiration, to distinguish it from respiration which requires air, or *aerobic* respiration.

The vast majority of organisms require air, and their respiration is aerobic. Germinating seeds afford a good illustration of the process of respiration in which the oxygen of the air is absorbed, or in which oxidation occurs. It is easily shown by experiment that sprouting peas take in oxygen, give off carbon dioxide and liberate heat. The amount of heat evolved and the carbon dioxide given off can be measured, and the quantity of either produced in a given time may be regarded as an index of the rapidity of the respiratory process.

Respiration is not confined to any part of the plant, but it takes place in all living cells. The plant needs energy in the building of protoplasm and for the work required in growth. The amount of work done by a growing plant is strikingly realized when the cumulative effect is seen. The pushing of seedlings through encrusted soil is a familiar illustration. Growing plants may lift a layer of concrete of considerable thickness, or a root of a bean encased in a plaster cast twice the thickness of the root will readily burst the cast (see Fig. 168). In the forest the roots of trees are seen to have split great ledges of rock, the accumulated energy required representing tons.

As to the heat evolved, the quantity is often very considerable, as in the case of germinating seeds which are richly supplied with stored food. In the large flowers of certain tropical plants (species of Arum) the amount of heat generated by respiration is sufficient to raise the temperature of the air within the flower 9 to 12 degrees above the temperature of the surrounding air. On the whole much less heat is evolved by respiration in plants than is the case in animals. It is a singular fact that most chemical changes take place in plants at a comparatively low temperature.

In all probability all the energy available to the plant with the exception of that required in photosynthesis is derived from processes of respiration and digestion. Respiration is a destructive process and not constructive; it does not store energy as in the food-making processes, but sets free the energy which was stored.

The prevailing view seems to be that respiration implies oxidation, and that the most efficient energy release is indicated by the amount of heat produced. It is well known that energy may be liberated by the decomposition of organic substances with the liberation of heat in other ways as well as by processes of oxidation. Berthelot found that, with the aid of platinum-black, formic acid, for example, may be decomposed with the liberation of heat, as expressed in the following equation:

formic acid		carbon dioxide		hydrogen
$HCOOH$	$=$	CO_2	$+$	H_2

The conclusion is that heat may be produced in living organisms without any connection with oxidation.

It must not be forgotten that many chemical changes can take place in plants at comparatively low temperatures, and that energy release does not necessarily imply the production of heat or oxidation. For plant life the processes included by the terms digestion, fermentation and respiration, function to one end, namely, the release of energy. It is conceivable that much of the oxidation observed has to do with the *elimination of waste products*, rather than with supplying heat or the liberation of energy.

TOPICS FOR REVIEW AND DISCUSSION

What are the processes by which food is built up?

What are the processes by which food is used and energy set free?

What are enzymes? May they be separated from the cells by which they are produced?

Name all the enzymes that you know about.

What is meant by the expression, "the action of an enzyme is specific"?

May a plant produce more than one kind of enzyme? Explain.

How are enzymes "killed"?

How may enzymes be preserved?

What is alcoholic fermentation? What are the by-products in the process?

Does the yeast plant produce more than one enzyme?

Explain how sweet cider is changed to hard cider. How is vinegar made?

Why is yeast used in the making of bread?

Name other economic processes in which enzymes play a role.

In what sense may one speak of the silo as the ox's kraut barrel?

What constitutes respiration?

What is the difference between respiration and breathing?

Do plants breathe?

What justifies the plant physiologist in saying that plants do not breathe?

What is aerobic respiration? Anaerobic respiration? Give illustrations.

In sprouting peas what indicates that respiration is going on?

What forms of energy are manifested by processes of respiration?

Compare the gaseous exchange in respiration and in photosynthesis.

Does respiration always imply oxidation?

Explain the meaning of the terms, anabolism, katabolism, and metabolism.

The farmer speaks of hay in the mow or grain in the stack "going through sweat." What happens?

What process takes place in the curing of tobacco?

Can one make vinegar from shavings and sugar?

What happens when milk sours? When butter spoils?

Why will kraut decay if exposed to air at ordinary house temperature?

Has enzymatic action anything to do with cheese making?

CHAPTER IX

GROWTH AND RESPONSE TO STIMULI

The term growth usually carries with it the idea of increase in size, which implies also an increase in weight of dried material. An increase in size of the plant, or any part of it, may not be accompanied, however, by an increase in dried substance; on the contrary, plants may lose in the weight of dried material while increasing greatly in volume, the increase in size being due to the accumulation of water, or *growth by hydration.* Seedlings grown for some time with their roots in clean sand or in pure water, especially if they are kept in the dark, will increase greatly in volume, but they will lose in dry weight. Some of the food substances present in the seed are consumed by katabolic processes involved in the release of energy. Growth under such conditions does not lead to the continued normal development of the plant, but to its exhaustion and death.

About half a century ago the distinguished botanist, Sachs, referred to growth as representing three phases: (1) the embryonic phase in which the beginnings of new parts are formed; (2) the phase of elongation, or enlargement of parts already formed; and (3) the phase of internal development, or the completion and maturing of the tissues. To use less formal statements, let us say that growth signifies the *forming*, *unfolding*, and *maturing* of the plant or of its parts. These three steps occur in the development of all plants, no matter how simple or how complex in structure.

It should be understood that these phases are not sharply separated in the plant as a whole, but they may merge into one another imperceptibly; for in a growing shoot in summer, the forming of new parts, elongation, and maturing of previously elongated parts go on simultaneously.

These three phases are well illustrated in the branch of a pine tree. During the previous season the bud at the end of the branch was formed (Fig. 165, left). At the growing point, there took place in the embryonic tissue of the end of the stem the division of cells and their arrangement into the primordia of the parts present, namely, scale leaves, dwarf branches and foliage leaves (needles), frequently flowers, and new buds. When growth begins in the following spring, these parts unfold, and the new shoot appears with an apparent suddenness (Fig. 165, right). The unfolding

is due to the increase in size of the cells, owing chiefly to the accumulation of water, or by hydration. This is the phase which is usually measured in growth-recording apparatus. It must be remembered that growth by accretion is likewise subject to measurement.

In many plants the total effect of growth by hydration is very striking, as when a mushroom "springs up in a night" because of the elongation of the cells of its stalk and cap; or when a bush becomes green with foliage in a day, as a result of the enlargement and unfolding of the parts in the

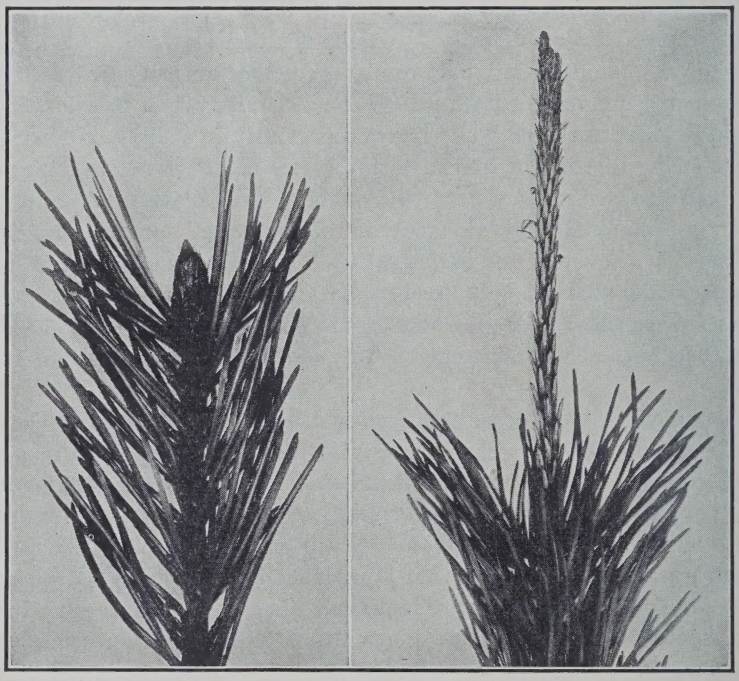


FIG. 165.—Part of a pine branch (left) ending in a winter bud. At the right the bud has unfolded into the long tender shoot with the elongating young leaves.

winter buds. It is said that the filaments of the stamens in the flowers of certain grasses (the bamboos) elongate as rapidly as the movement of the minute hand of a watch. In the case of the bamboo, however, the growing zone is of considerable length, involving a large number of cells, whereas the percentage of growth is much lower than in the case of certain fungal filaments and pollen tubes in which but one or only a few cells are concerned. The part of the plant that elongates in root or shoot, for example, may be readily located by placing on it at definite distances marks made with water-proof ink, as shown in Fig. 166, A. The root of a seedling so marked will appear after 24 hours as shown in Fig. 166, B.

Where no elongation has taken place the marks remain the same distance apart as at the beginning of the experiment; but in the elongated portion

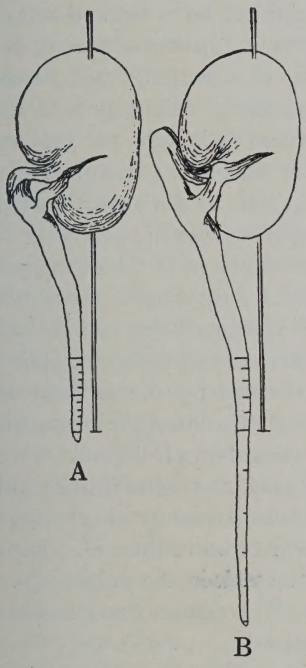


FIG. 166.—Region of elongation of growing root of seedling of the broad Windsor Bean (*Vicia faba*). A, the end of the root is marked with water-proof ink at intervals of 1 mm. B, the same root 24 hours later. The greater distances between the marks indicate that the region of greatest elongation lies within the first four or five millimeters back of the root cap. (Strasburger, Macmillan Co.)

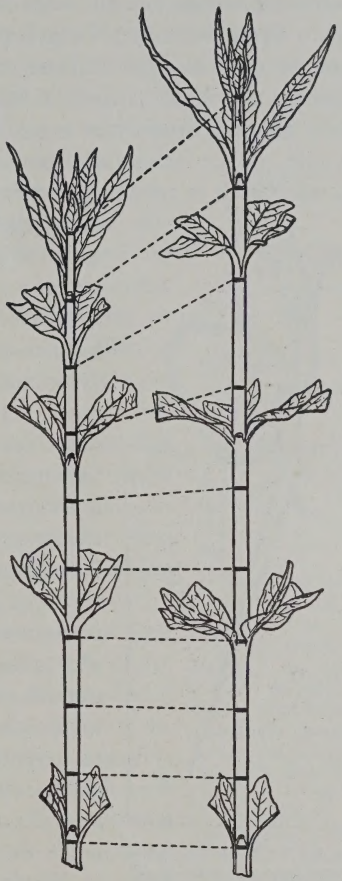


FIG. 167.—The region of elongation in the stem (*Lysimachia vulgaris*). Where the marks are evenly spaced on both stems no elongation occurred. The part elongated is shown at the right by the greater spaces between the corresponding marks on the stem. (From Ganong's, "Textbook of Botany," Macmillan Co.)

distances between the marks have very noticeably increased. Thus we see that in a root the region of elongation is confined to a portion a few millimeters in length just back of the apex covered by the root cap.

In like manner the region of elongation in a stem is found to be confined to a length of a few internodes back of the growing point (Fig. 167).

Following elongation, the cells of the larger part of the branch or root mature. Their walls may be greatly thickened, and food may be accumulated in certain cells. These are processes of the accretion of dry substances, as distinguished from hydration. The ends of growing members such as stems and roots are characterized by the presence of embryonic cells. In gymnosperms and in dicotylous angiosperms, embryonic tissue is continued back into the older parts between phloem and xylem, where we have learned to know it as cambium. Cells capable of growth and division occur also in older and adult tissues.

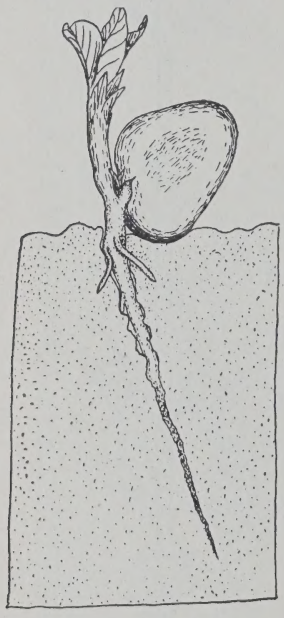


FIG. 168.—Mechanical work done by a growing plant. Root of Windsor bean bursting a block of gypsum in which the root was embedded.

Root Contraction.—While growth usually implies an increase in length, yet just the reverse may occur during the maturing of some roots. The tap root of the broad bean (*Vicia faba*), for example, shortens appreciably during the internal development of the older parts, as is evidenced by a wrinkling of the surface of the root a short distance below the cotyledons. The phenomenon is known as *root pull*. The shortening is effected by the increase in the transverse axes of the cells of the cortex and the shortening of their longitudinal axes. A notable example is found in the Skunk Cabbage, in which the older roots by shortening tend to keep the stem down in the soil. Root pull occurs also in the jack-in-the-pulpit (*Arisaema triphyllum*), in the common dandelion, and in many other plants.

Work Done in Growth.—The work done by growing organs is often very great, as measured by its cumulative effect. Roots of trees pry apart ledges of rock or split off fragments requiring an amount of energy equivalent to the lifting power of tons. By a simple experiment the root of a bean may be shown to develop sufficient energy to split a plaster cast (Fig. 168). Or the growing leaves of a fern are known to be capable of lifting a thin crust of overlying concrete. Instances of the work done by growing roots and stems are frequently encountered.

PLANT RESPONSES

One of the most marked differences between living organisms and inert objects is the fact that the former respond to stimuli in a manner very

different from the reactions of non-living matter. Plants and plant parts adjust themselves to one another, to their immediate neighbors, and to forces of the environment that affect them as stimuli.

Motile plants, or motile plant cells, manifest their response in changes in the direction of locomotion, while those that do not have the power of locomotion respond by means of growth curves. The response made to a given stimulus is usually designated by a term implying the character of the stimulus, as, for example, the response made by a plant organ to gravity is termed *geotropism;* to light, *phototropism;* to moisture *hydrotropism*, etc. When the direction of the response is toward the source of the stimulus, it is designated as *positive*, or *pro-*. A response in the opposite direction, or away from the source of the stimulus, is *negative*, or *apo-*. A few plant responses will be dealt with in the following paragraphs.

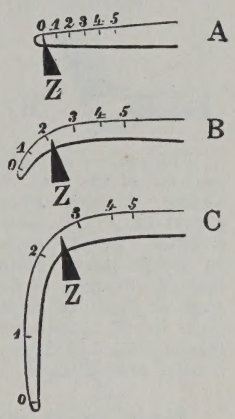


FIG. 169.—Geotropic response of the primary root of the Windsor bean (*Vicia faba*) A, the root marked off with waterproof ink at intervals of 2 mm is placed in a horizontal position; B, the same after 7 hours; C, after 23 hours. Z, the stationary index. The root curved perpendicularly downward, and the region which curved is the region which elongated. (Strasburger, Macmillan Co.)

Geotropism.—Plants adjust themselves to the force of gravity. Primary roots tend to grow toward the center of the earth. They are positively geotropic. Stems which grow in the opposite direction are negatively geotropic. Roots or branches growing horizontally are *diageotropic.*

It is readily shown by experiment that if a root or a stem be inclined from the normal vertical position with reference to gravity, as when placed horizontally, the root will curve downward and the stem upward. The place of curvature will coincide with the region of greatest elongation; hence such curves are growth curves (Fig. 169). The curving organ elongates faster on the convex side than on the concave side. In fact the concave side is often shortened. In the case of the root, the stimulus of gravity is perceived by the growing point and the root cap, and transmitted to the region of elongation where curvature takes place. If the tip of the horizontally placed root be cut off carefully with a sharp razor, the root will elongate, but it will not curve until by regeneration a new growing point is established.

A stem twines about a support as shown in Fig. 119 by virtue of a response to gravity, which has been called *lateral* geotropism.

Stems of grasses are of interest in that the curvatures occur in older parts which are not elongating, but which are capable of growth. Such parts are located at the base of the internodes. A piece of a stem including

at least one joint is placed in a horizontal position (Fig. 170, A). After 24 hours the part above the joint is bent upward at an angle of about 75° (Fig. 170, B). The lower side of the joint (*u*) has increased in length, while that of the upper (*o*) has been shortened by pressure and loss of water. In this manner stems of fallen grain tend to right themselves. The older part of the stem of the spiderwort (*Tradescantia*) behaves in a similar manner.

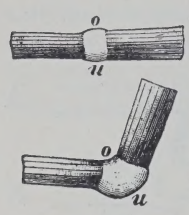


FIG. 170.—Geotropic response of the stem of a grass. A, node of stem placed in a horizontal position. B, the same 24 hours later. Note that the bending at an angle of about 75° took place at the joint, the growing region. (Strasburger, Macmillan Co.)

Some plant organs respond negatively in one stage of development and positively at another stage. The flower stalk of the peanut plant is negatively geotropic before and at the time of blooming, but positively geotropic after blooming, when the end of the pedicel grows down into the soil where the legume called a peanut develops.

Phototropism, Response to Light.—In the chapter on leaves attention was directed to the light position of leaf blades as manifested in the leaf mosaic, the rosette habit, and in the compass plants. All such phenomena are the expressions of phototropic responses.

Plant organs which are positively phototropic in one stage of their development and negatively phototropic in another, are not uncommon. The flower pedicel of the Kenilworth ivy (*Linaria cymbalaria*) positively is phototropic at the time of the opening of the flower, but as the fruit is maturing the pedicel becomes negatively phototropic and thrusts the seed pod into a crack or cranny of the substratum.

A combined geotropic and phototropic response may be demonstrated by placing an inverted plant near the window in a room where the adjustment of leaves and stems involves responses to both light and gravity.

Response to Contact, Thigmotropism.—We have learned that the Virginia creeper clings to a wall or other flat surface by means of its tendrils and roots, and that certain tendrils of other plants wind about a support. The clasping organs are able to attach themselves, as already described, by virtue of their sensitiveness to contact.

Response to Injury, Traumatropism.—The response which a plant makes to injury of any sort is known as *traumatropism*. If a bit of stiff paper be glued to one side of the growing tip of a root, or if the growing point be injured by cutting away with a sharp razor a thin tangential section, or by searing with a hot glass rod, and the seedling with the root thus injured be supported in moist air so that growth will continue, after several hours the end of the root, in successful experiments, will have made a sharp curve away from the injured side (Fig. 171).

Hydrotropism and Rheotropism.—That roots seek moisture is a well known phenomenon. Those of the willow and Carolina poplar are unusual in their tendency to enter and clog drain pipes and break through the walls of cisterns, if but the smallest openings are available. In the garden and in cultivated fields, the most copious development of roots is found in those parts of the soil where moisture is abundant.

An experiment set up as shown in Fig. 172, or in some similar manner, will demonstrate the response of roots of seedlings to moisture. The majority of the roots will follow the moist surface instead of continuing straight downward.

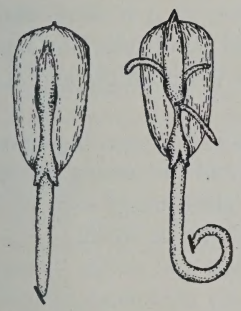


FIG. 171.—Response made to injury by a growing root. A small bit of paper fastened to one side of the tip of the root causes the root to curve in growth away from the source of irritation. A, at the beginning of the experiment. B, 24 hours later.

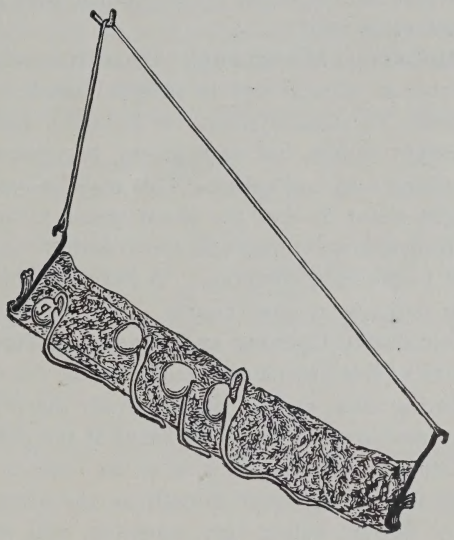


FIG. 172.—Apparatus for demonstrating hydrotopism. A box-like container, made of wire netting (¼ inch mesh) and filled with moist sawdust in which peas are planted, is supported in an inclined position. The roots of the seedlings at first descend into the air but soon turn toward the damp sawdust. (Palladin.)

The response which roots make to currents of water is called *rheotropism.*

Chemotropism, Chemotaxis.—Responses made to stimuli resulting from chemical substances are many and varied. Certain reproductive cells of many plants are very sensitive to dilute chemical solutions. The sperm of the fern, for example, is known to respond to various chemical

substances under experimental conditions in the laboratory. They will flock into a capillary tube containing a dilute solution of malic acid (.1% to .001%) with the same alacrity as they enter the plant organ containing the egg with which the sperm normally unites (see life history of the fern).

Various kinds of plants grow in the direction of food supply, because of the response to chemical substances. The pollen tube makes its way unerringly through parts of the pistil to the egg in the ovule in response to some chemical in the ovule or in the egg.

When the responses are concerned with free swimming cells the term *chemotaxis* is used.

Autonomic Movements.—There is another class of movements not due to external stimuli but to internal causes. One of these is known as *nutation*. A stem or shoot, for example, does not grow upward following a straight course, but as it grows, it continually curves in one direction, describing a sort of spiral. This may be recognized in a rapidly growing upright shoot in that the shoot seems to lop over as if it were wilting. Continued observation will show that the curved shoot does not always point in the same direction. A record of the movement of the end of the shoot indicates a spiral course.

Successive Opening and Closing of Flowers.—The opening of such flowers as the Crocus and Tulip during the day and the closing at night, or during cool, cloudy daylight, are due to alternating growth on the upper and lower sides at the bases of the parts of the perianth.

Growth on the upper side of the bases of sepals and petals (*epinasty*) opens the flower, while growth on the lower sides (*hyponasty*) closes it. Many flowers being very sensitive, will respond to slight changes in temperature.

There are many kinds of plant responses, but those mentioned in the foregoing will serve to illustrate the manifold sensitiveness of living things.

TOPICS FOR REVIEW AND DISCUSSION

What is meant by the expression, growth by hydration? Growth by accretion? Give illustrations of each?

May a plant grow and lose in dry weight? Explain.

Who was Sachs? For what was he famous? When did he live?

What are Sachs' three phases of growth? Explain, using a winter bud as an illustration.

How rapidly may some plants elongate in growth?

What is "root pull"? Explain how you think it is accomplished.

Does root pull play an important role in the economy of the plant?

Name plants in which root pull is easily recognized.

May growing plants do work of a mechanical nature?

What is a stimulus?

What is meant by saying plants are sensitive or irritable?

Name all the stimuli you know to which plants respond. Name all the responses you have observed.

What is a positive response? A negative response?

Have plants special senses?

What is a special sense?

How many special senses have human beings?

How many special senses have plants?

What is the difference between animal vision and a plant's response to light?

Do plants manifest psychological phenomena?

May a stationary plant organ move or curve without growth?

Explain how a tulip or crocus flower opens and closes? Does the environment have anything to do with the closing or opening of flowers?

The blossom of the peanut plant is borne above ground, but the fruit matures in the soil. Explain. Do you know of other similar phenomena?

Do you know of any plant movement which is not a response to some stimulus of the environment?

What enables a twining stem to wind about a support?

Name some plants whose stems twine clockwise. Name some which twine counter clockwise.

Why does the morning glory twine left-handed and the hop vine right-handed?

Would you select the same kind of a support for a pea plant as for a pole bean?

Why are roots of trees prone to enter drain tile and sewer tile?

Is there a relation between the spread of the roots in the soil and the watershed formed by the leaves of any plant you know?

If a young potted bean plant be turned upside down, the leaves will right themselves. How do they do so? Why do they do so?

How do ordinary leaves execute their night and day position?

How does the sensitive plant (Mimosa) execute the day and night position of its leaves?

Will the wild lettuce plant (*Lactuca scariola*) show the characteristic of a compass plant if it be grown in the shade?

Does any plant have a sense of touch or contact? Would a sense of contact be of any value to the plant?

Distinguish between hydrotropism, hygrotropism, and rheotropism.

What enables fallen grain (wheat, oats, etc.) to right itself?

Is the ability to respond to injury of any value to the plant?

When is the term chemotaxis used instead of chemotropism?

Is there a much greater development of the root system in moist soil than in dry soil?

Will roots grow deeper in a dry season than in a wet season?

Why will a horizontally placed root end not bend downward if the tip be cut off?

What part of the root perceives the stimulus of gravity? What part gives the response?

Does the older stem of a Virginia creeper cling to a tree trunk in the same way that the young stems do?

What enables the growing end of a sunflower stem to tend to follow the sun?

CHAPTER X

THALLOPHYTA—MYXOMYCETES, SCHIZOPHYTA

Introduction.—The preceding chapters have been concerned with the structure and function of the three members of higher plants, namely, leaf, stem, and root. The following will deal chiefly with selected life-histories, beginning with the lowest and simplest plants and proceeding through the several groups to the highest.

Classification of Plants.—All individual plants which closely resemble each other in structure and life-history are designated as of the same kind or *species*, and each species known to science is given a name consisting of at least two words, one representing the *generic* name and the other the *specific* name. For example, the scientific name of the Maidenhair fern is *Adiantum pedatum*, Adiantum being the generic and pedatum the specific name. A genus includes all those different species which have certain characteristics in common. The species of a genus are supposed to be closely related. The genera having certain characteristics in common are brought together in a family, and related families constitute an order. Orders in turn are included in larger assemblages, such as classes, subdivisions, groups, etc. Using the Maidenhair fern again as our illustration, we find that it belongs to the

Group, Pteriodphyta,
Order, Filices,
Family, Polypodiaceae,
Genus, Adiantum,
Species, pedatum.

Usually in writing the scientific name, the initial, or some other abbreviation of the last name of the person accredited with having described the plant is placed after the specific name thus, *Adiantum pedatum* L., the "L" standing for the name, Linné (Linnaeus). Scientific names are usually derived from Greek or Latin words, or made from Latinized words or expressions taken from other languages.

It is generally assumed that a genetic relationship exists among all plants, and the aim of a natural system of classification is to express the degree of this relationship. The ideal natural classification would enable us to construct a true family tree of the vegetable kingdom, but such a classification is not to be hoped for, because of the fact that many plant-forms which existed in the past have completely disappeared, and of those

which have become extinct, relatively few have left well preserved remains in geologic deposits. The disappearance of large portions of the flora of the past has left isolated surviving types which seem only distantly related to other known forms. Of the isolated groups may be mentioned the Diatoms and the Charales.

Those features which are of first importance in determining relationships are structure and reproduction as revealed in the complete life history. Reproductive structures are especially valuable, because they are less variable and less subject to change from external conditions. As will be pointed out in the following chapters, those plants, for example, which possess the reproductive organ known as an archegonium are unquestionably related. It is assumed also that the life history (Ontogeny) of certain individuals repeat, to a certain extent, the developmental history of the race to which they belong (Phylogeny), and consequently such life histories are valuable in determining relationships and the trend of that progressive development known as evolution.

The following simplified classification of the plant kingdom may be found convenient and useful:

GROUP THALLOPHYTA

Subdivision I.	Myxomycetes	Slime Moulds
Subdivision II.	Schizophyta	Fission Plants
Class 1.	Cyanophyceae	Blue-green Algae
Class 2.	Schizomycetes	Bacteria
Subdivision III.	Flagellateae	Euglena (?), Peridinium
Subdivision IV.	Zygophyceae	
Class 1.	Bacillariales	Diatoms
Class 2.	Conjugateae	Pond Silks, Desmids
Subdivision V.	Chlorophyceae	Green Algae
Class 1.	Volvocales	Rolling Algae.
Class 2.	Protococcales	Green Films
Class 3.	Confervales	Confervoid Algae
Class 4.	Siphonales	Green Felts
Subdivision VI.	Charophyta (Charales)	Stoneworts
Subdivision VII.	Phaeophyceae	Brown Algae
Subdivision VIII.	Rhodophyceae	Red Algae
Subdivision IX.	Eumycetes	Fungi
Class 1.	Phycomycetes	Algal-Fungi
Class 2.	Hemiascomycetes	Yeasts
Class 3.	Ascomycetes	Sac Fungi
Class 4.	Basidiomycetes	Basidia Fungi
Class 5.	Lichens	

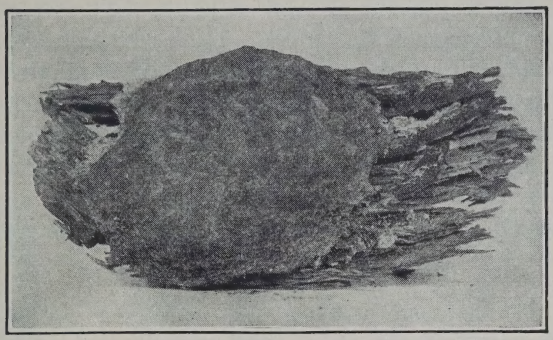
	GROUP BRYOPHYTA	
Class 1.	Hepaticeae	Liverworts
Class 2.	Musci	Mosses
	GROUP PTERIDOPHYTA	
Class 1.	Filicineae	Ferns and Fern-like Plants
Class 2.	Equisetineae	Horse Tails, Scouring Rushes
Class 3.	Lycopodineae	Club Mosses
	GROUP SPERMATOPHYTA,	Seed-bearing Plants
Class 1.	Gymnospermae	Cycads, Pines, Cedars, Hemlock, Cypress, Arbor Vitae, Gnetum
Class 2.	Angiospermae	Flowering Plants
Subclass	Monocotyledonae	Monocotylous Plants
Subclass	Dicotyledonae	Dicotylous Plants

MYXOMYCETES (SLIME MOULDS) AND SCHIZOPHYTA (FISSION PLANTS)

The slime moulds comprise a group of low organisms on the border line between plants and animals. In their vegetative, or assimilative, phase, called the *plasmodium*, they bear certain resemblances to the microscopic, one-celled animal, the amoeba; but in the reproductive, or spore-producing, phase they reveal very definite and pronounced plant characteristics. In their reproductive phase the larger forms are commonly recognized as yellowish or light-colored, cake-like masses on such objects as decaying logs and stumps, saw dust, the planks of walks, spent tanbark, decaying leaves, and apple pomace. These large spore-bearing masses may have a brittle, limy crust, as in Fuligo (Fig. 173, A), while in others the mass is provided with a firmer, skin-like cover, as in Lycogola (Fig. 174, A). In the spore-producing phase some of the large species were mistaken by the earlier botanists for puff-balls.

The vast majority of the slime moulds, however, develop small and very beautiful reproductive bodies that are recognized only by those having had some training in their observation.

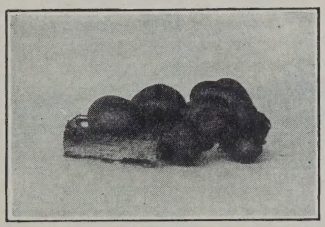
The Plasmodium, or Vegetative Phase.—The plasmodium of a typical slime mould consists of a naked, multinucleated mass of cytoplasm that creeps or flows through the crevices and interstices of the decaying wood, leaves, soil or other substratum on which it happens to be growing. Generally the plasmodium appears as a thick, sticky or slimy, yellowish or creamy mass within the substratum, or as it moves out upon the surface.



A

B

FIG. 173.—Fruiting phase, or spore-bearing part, of slime mould. A, *Fuligo ovata* (Schaeff.) Macbr.; B, *Stemonitis morgani* Peck. × 1.



A

B

FIG. 174.—Spore-bearing part (sporangia) of slime mould on decaying wood. A, *Lycogola epidendrum* (Buxb.) Fr.; B, *Hemitrichia clavata* (Pers.) Rost.

Though the color be prevailingly yellow, it may be brown, red, violet or almost any tint, even greenish. In Fig. 175, there is represented a portion of a plasmodium which crept over the inner surface of the wall of a bell jar used as a cover for a piece of decaying wood on which the plant was growing. The piece of wood was placed under the bell jar in the evening, and the next morning the plasmodium was found thus spread out upon the glass in a very intricate, vein-like network. This illustrates the manner in which the plasmodium flows through the interstices of the

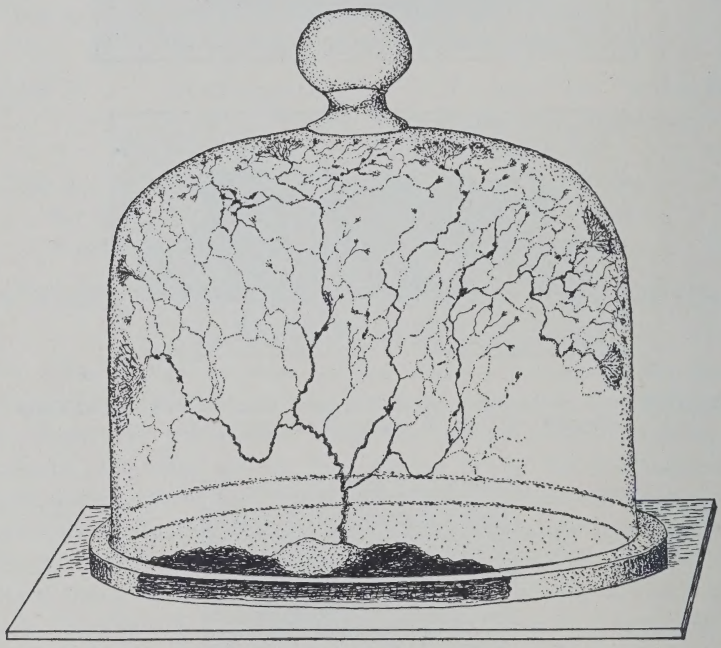


FIG. 175.—Plasmodium of a slime mould (Fuligo) spread over the inner surface of a bell jar from a piece of decaying wood; the result of 36 hours' growth. × ⅓.

decaying wood or other substratum. The plasmodium creeps by sending out extensions in various directions, and these extensions may anastomose to form a complicated network. Fig. 177, K represents a portion of the plasmodium enlarged. When observed in laboratory cultures the small plasmodia resemble in structure and movement a giant amoeba. Plasmodial masses twenty to thirty centimeters in diameter, and almost half a liter in volume, have been found on decaying apple pomace.

With some exceptions, to be mentioned below, slime moulds are saprophytes; that is, they live on, and obtain their food from, *dead* organic matter.

Under certain conditions, as low temperature or lack of moisture, the plasmodium may pass into a dormant phase, forming a firm, dry lump of considerable size known as a *sclerotium*. These lumps may sometimes be divided into polyhedral masses, or cells, with cellulose walls. On the return of favorable conditions the cell walls will dissolve, and active growth will be resumed.

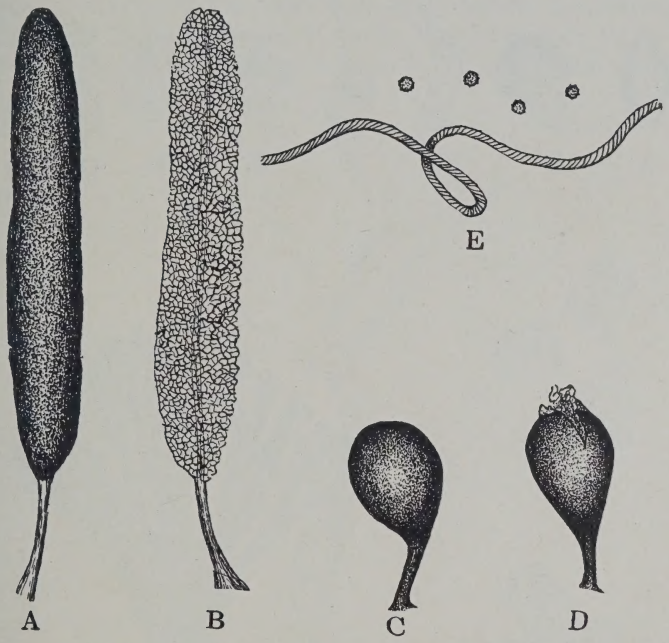


FIG. 176.—Individual sporangia of slime mould greatly enlarged. A, B, *Stemonitis morgani* Peck. A, surface view; B, sporangium with spores dusted out, showing the fine net-like skeleton, the capillitium; the stalk, continued up through the capillitium, is known as the columella. C, D, E, *Hemitrichia clavata* (Pers.) Rost.; C, unopened; D, opened; E, spores and a piece of an elater.

The Fruiting Phase.—As already mentioned, the fruiting phase involves the spore-bearing condition. When ready to produce spores, the plasmodium, which has thus far shunned the light, flows out of the interstices of the substratum into the light and collects into masses upon its surface, or creeps upon sticks, stones, or other objects lying upon the substratum, or upon the stems and leaves of plants, if the substratum be the soil. From these masses the spore-bearing bodies (sporangia) are formed. In species (Fuligo, Fig. 173, A) that live upon tan bark, decaying wood, or apple pomace, the spore-bearing structure is in the form of large cake-like masses. Figs. 174, A and 176, A, B, C, D, represent sporangia of common genera. Each sporangium consists of numerous spores held

in a delicate network, the *capillitium*, which is not made of cells, but of dried and transformed cytoplasm. Fig. 176, B shows the capillitium in Stemonitis after the spores have been dusted out. It consists of a threadwork supported by a slender stalk, the *columella*.

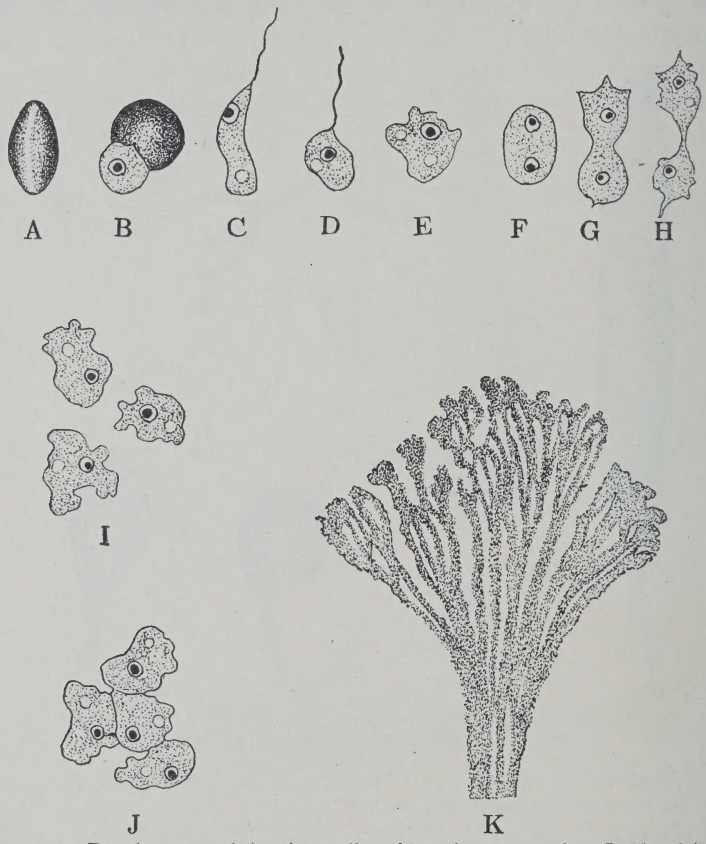


FIG. 177.—Development of the plasmodium from the spore. A to J, *Chondrioderma difforme*. A, spore; B, germinating spore; C, swarm cell; D, swarm cell changing to a myxamoeba, E; F–H, division of myxamoebae; I, J, myxamoeba fusing; K, small terminal plasmodial fan of the plasmodium shown in Fig. 175. (A–E, I, and J, Strasburger, Macmillan Co.; F–H, after Brefeld.) × 500.

Life History.—Under proper conditions of moisture and warmth, the spores* will germinate. They absorb moisture, increase in size, and as a result the walls break open. The contents of each spore escape as a swarm cell with one cilium or, in certain species, as an amoeboid cell

* For our purpose a *spore* may be defined as a specially formed cell which separates from the parent plant, and which by itself is capable of growth and division to form an individual. The spores of some plants may consist of two or more cells.

(Myxamoeba) (Fig. 177, A-E). The swarm cell moves about actively for a time, finally withdrawing the cilium and assuming the amoeboid form. The myxamoebae continue their amoeboid movement, increase in size, and divide (Fig. 177, F, G, H). The new cells in turn grow and divide, division and growth continuing for some time, depending upon conditions of nutrition. The large number of myxamoebae finally unite into a common cytoplasmic mass with many nuclei, the plasmodium (Fig. 177, I, J). In the formation of spores, the plasmodium by the process of division by surface cleavage furrows is broken up, first into larger

FIG. 178.—Seedling of cabbage plant showing "club root" caused by the parasite, *Plasmodiophora brassicae* Woronin. × 1.

multinucleated masses, which in turn give rise by continued cleavage into smaller and smaller masses, resulting finally in the minute uninucleated cells, each of which develops a cell wall and becomes a spore.

The fusion of nuclei in pairs in the plasmodium of some species at a stage prior to the formation of spores has been reported by certain observers. This phenomenon is known as *karyogamy*, and it bears a resemblance to the fusion of nuclei in the union of gametes in higher plants.

Although nearly all of the 500 species of slime moulds are saprophytes, a few are parasitic upon higher plants. Among the latter, one species (*Plasmodiophora brassicae* Woronin) is parasitic upon the cabbage, causing the disease known as "club root" (Fig. 178). Another species

(*Spongospora subterranea* (Wallr.) Johnson) produces "powdery scab" of the white or Irish potato.

FISSION PLANTS—SCHIZOPHYTA

The fission plants constitute a group of organisms of simple structure in which the fundamental distinguishing characteristic is the division of the cells by simple fission. This is the chief method of multiplication or propagation. In the majority of them, under certain conditions, special cells may be formed that function as spores, but these cells in many cases resemble the vegetative cells too closely to be regarded as typical spores. The individuals exist as single cells, colonies, or filaments. There are two classes of Schizophyta, the Cyanophyceae (Blue-Green Algae), which contain chlorophyll, and the Schizomycetes (Bacteria), which are devoid of chlorophyll.

BLUE-GREEN ALGAE—CYANOPHYCEAE

The Blue-Green Algae are distinguished in general by their blue-green color, which is due to the presence of the bluish pigment, *phycocyanin*, in the protoplasm along with chlorophyll. Phycocyanin is soluble in water in dead cells. If a mass of the plants be dried and pulverized, to kill the cells, and placed in water, the blue coloring matter will be dissolved out. When the water is filtered off and the residue treated with alcohol, a greenish-yellow color will be dissolved in the alcohol, indicating the presence of chlorophyll.

It is of interest to note that not all Cyanophyceae are blue-green in appearance. Some are reddish, and some are yellowish.

The Cyanophyceae live both in fresh water and in the sea, sometimes occurring in such quantities as to impart their characteristic color to the water. The name, Red Sea, is said to have been given that body of water from the reddish hue imparted to the surface of the water by the presence of myriads of the blue-green alga, *Trichodesmium erythraeum*. Like many other lower plants they have an extremely variable habitat. They may be found upon moist earth, stones, or other objects, in ponds and streams containing decaying organic matter; in the roots of cycads and other seed plants; in the air spaces of aquatic ferns (Azolla); and within the bodies of certain liverworts. Some constitute the algal constituent of certain lichens (Collema, Peltigera).

Gloeocapsa.—Let us now become better acquainted with the life of blue-green algae by the consideration of a few samples or type forms. One of the simplest is Gloeocapsa. It exists as single cells or cell colonies*

* A cell colony consists of two or more cells loosely held together. These cells may be alike in structure and potentially equal in function. Colonies may be indefinitely

surrounded by a stratified, mucilaginous or jelly-like substance, as in Fig. 179, A, B, C. The stratified, gelatinous substance aids one in distinguishing Gloeocapsa from other unicellular blue-green algae. The gelatinous material is derived from the cell wall. The cell contents appear blue-green and densely granular. The pigments are located in the layer of cytoplasm next to the cell wall, and this layer is sometimes regarded as the chloroplast, which is in the form of a hollow sphere or cylinder. Seldom in the Cyanophyceae do we find definite and sharply defined chloroplasts as in most

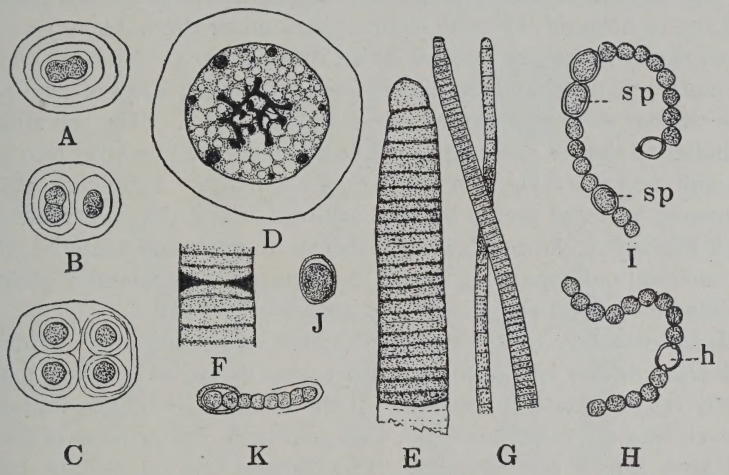


FIG. 179.—Blue-Green Algae. A–C, *Gloeocapsa polydermatica*. A, single cell in which division has begun; B, two cells resulting from fission; the cell on the left is dividing; C, colony of four cells; D, fixed and stained cell of *Rivularia pisum*. The net-like central body is the nucleus. × 3000. E, F, *Oscillatoria princeps* Vaucher. E, terminal portion of a filament; F, portion of a filament showing an injured cell. × 540. G, a smaller species of Oscillatoria. H–K, Nostoc. H, portion of filament; *h*, heterocyst; I, portion of a filament with spores (*sp*); J, spore; K, short filament produced by germinating spore. × 650. (A to C, after Strasburger; D, after Haupt; H, I, J, K, after Bornet.)

plants containing chlorophyll. But in the genera Glaucocystis and Chrotheca well differentiated chloroplasts occur. The product of photosynthesis is said to be glycogen. In the cells of many of the blue-green algae, probably in Gloeocapsa, there is in the center of the cell a body which is regarded as a nucleus (Fig. 179, D). In active vegetative cells the nucleus is usually found in some state of division, and for that reason a nuclear membrane, if present, might not always be observed. On the whole, it

organized, that is, with the cells all alike and held together without any definite and fixed arrangement, or definitely and more highly organized, with the cells arranged in some rather definite and fixed pattern. In the latter case the cells may differ somewhat in structure.

seems evident that the cell here is less highly specialized than in higher plants. The cell structure has been studied in but a few forms. Fig. 179, D shows a stained section of a cell of Rivularia. The irregular structure in the center of the cell represents the necleus; the dark round objects near the periphery represent glycogen granules. It is probable that the structure of Gloeocapsa is similar to that of Rivularia.

Oscillatoria.—Oscillatoria is one of the simplest filamentous blue-green algae. It is common in ponds, streams, and moist places in which the water contains decaying organic matter. It forms floating masses or coatings or films on the earth or on objects under the water.

In the large species selected as an illustration (*O. princeps*) the cells are much broader than long, the filament resembling a row of coins placed with the flat sides together, as shown in Fig. 179, E. The cell structure is similar to that of Gloeocapsa. The pigments are in a layer next to the cell wall, and this layer is in the form of a cylinder. Frequently granules of reserve material are to be seen arranged along the transverse walls. Each filament is surrounded by a sheath of gelatinous material, which, by swelling and expanding, helps to produce the progressive gliding or crawling movement so noticeable in species of this genus.

It is customary to speak of the filament as an individual. However, each filament may be looked upon as a colony of similar cells held together chiefly by the gelatinous sheath. If the filament be broken into pieces, or even into the individual cells, each uninjured cell or piece of filament will grow into a new filament. The filament has no definite base or apex. There may be some coöperation of the cells in the movement, and it is in the movement that the filament acts as an individual.

Nostoc.—A mass of Nostoc consists of filaments of beadlike, blue-green cells. At intervals in the filaments there are slightly larger, round, yellowish cells with thicker walls. These are the *heterocysts*, or limiting cells. As a rule they do not divide, and their function is unknown (Fig. 179, H, *h*). The gelatinous sheath of the filament is usually very thick, and the many sheaths together form the thick masses of jelly in which the plant is usually found. Sometimes in relatively pure water, these large, rounded masses, with uneven, lumpy surfaces, may attain the size of a lemon or small orange.

Anabaena.—Anabaena resembles Nostoc and it is often found floating in water along with Nostoc (Fig. 180, A, B). It differs from Nostoc in that the filaments are usually straight and devoid of a sheath. They do not, therefore, form large, firm gelatinous masses, but a thin, mucus-like stratum. The heterocysts are numerous and are generally distributed along in the filament. The spores are much larger than the vegetative cells. They may occur singly, or one on each side of the heterocyst, or,

rarely, in continuous rows or chains. Certain species live in the intercellular spaces of the leaves of small floating aquatic ferns such as Azolla.

Cylindrospermum.—Cylindrospermum differs from Nostoc in that the filaments show some tendency to be differentiated into base and apex, and the cells are less rounded. Just above the heterocyst is formed a large spore (Fig. 180, C, *s*). Cylindrospermum does not form masses of jelly like those of Nostoc, but slimy films that spread over the surface.

Rivularia.—Rivularia forms globular or irregular masses of jelly in which the filaments are arranged somewhat radially. At the base of

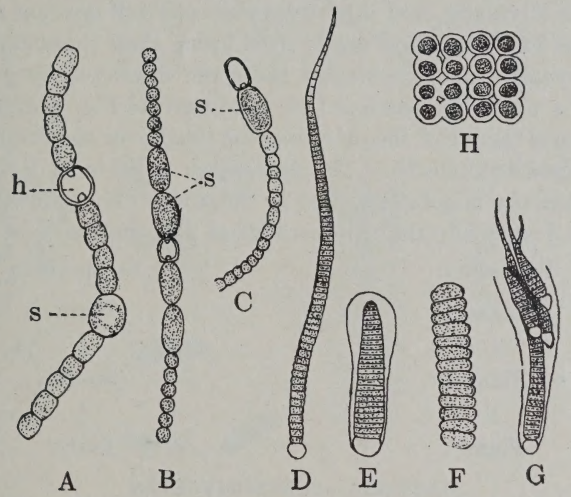


FIG. 180.—Blue-Green Algae. A, *Anabaena azollae* Strasb.; B, *Anabaena inequalis* (Kutz) Born. and Flah.; C, *Cylindrospermum catenatum* Ralfs.; *h*, heterocyst; *s*, spore; D–G, *Rivularia bullata* Berk.; D, Single filament; E, F, hormogonia; G, formation of hormogonia; H, Merismopedia. (A, C, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Co., Publishers. B, from "A Treatise on the British Freshwater Algae." By the late G. S. West; revised by F. E. Fritsch, Cambridge. University Press, 1927; D–G, after Bornet, from Engler and Prantl.)

the filament is a heterocyst, above which a spore may be formed. The filaments end in long, slender, colorless cells. These filaments are differentiated, therefore, into base and apex, and contain three kinds of vegetative cells (Fig. 180, D).

Merismopedia is in the form of square or rectangular plates of cells, due to the regular division of cells in two planes at right angles to each other (Fig. 180, H).

Vegetative Propagation.—By vegetative propagation is meant the division or separation of any part of the plant to form another individual. If the plant be unicellular, the simple division of the cell accomplishes vegetative propagation; if multicellular, a separation of any vegetative part to become another individual constitutes vegetative propagation.

With certain notable exceptions, almost all plants may be propagated vegetatively.

In the Cyanophyceae, vegetative propagation, which in some forms is the only method known, consists of the simple fission of the cells. In certain filamentous forms there is another method in which a piece of filament escapes from the gelatinous mass, moves away a short distance, and develops into another plant. Such pieces of filaments are called *hormogonia* (Fig. 180, E, F, G).

Propagation by Spores.—In some blue-green algae, as Nostoc, Cylindrospermum, Rivularia, and others, certain cells will develop a thick cell wall and pass into a dormant state, often losing their characteristic color. These are *spores*. On germination the spore develops, by growth and fission, into a plant like the one that produced it (Fig. 179, J, K). By means of spores the life of the plant may be tided over conditions unfavorable for vegetative growth. The spores are capable of living on dry land, and when dry may be scattered by the wind. The following diagram will indicate graphically the two methods of propagation:

By fission:	By spores:
Plant	Plant
↓	↓
Plant	Spore
↓	↓
Plant	Plant

BACTERIA—SCHIZOMYCETES

Bacteria are unicellular fission plants devoid of chlorophyll, hence called *Schizomycetes* (fission fungi). With some notable exceptions they are either parasites or saprophytes. They are among the simplest and smallest of all living things, some of the globular forms being less than one micron (1/25,000 inch) in diameter. Individual bacteria appear colorless, but, in large colonies or masses, various species exhibit bright colors. For example, one species growing on bread (*Micrococcus prodigiosus*) forms blood-red specks or patches. Those which exhibit colors in this way are called *chromogenic* bacteria.

In the form of the cell some bacteria are globular, and such are designated by the collective term *cocci*,* as Micrococcus, Staphylococcus, etc. Those in the form of straight rods belong generally to the genus Bacterium, if non-motile, and to Bacillus (Migula) if motile.[1] Rod-

* Coccus, pronounced cok'kus; but cocci, cok'si.

[1] Erwin Smith included in the genus Bacterium non-motile rod-shaped forms and those possessing cilia at the end. Those that bear cilia scattered over the cell are placed in the genus Bacillus.

shaped forms with a slight spiral curve are called Vibrio, and those more strongly curved, Spirillum. Certain straight filamentous forms are termed Leptothrix and the spirally wound filaments, Spirochaete.

Many bacteria are actively motile, due to the presence of one or more cilia, which may be borne at one or both ends, or distributed over the entire surface of the cell. Some bacteria, as the hay bacillus (*Bacillus subtilis*)

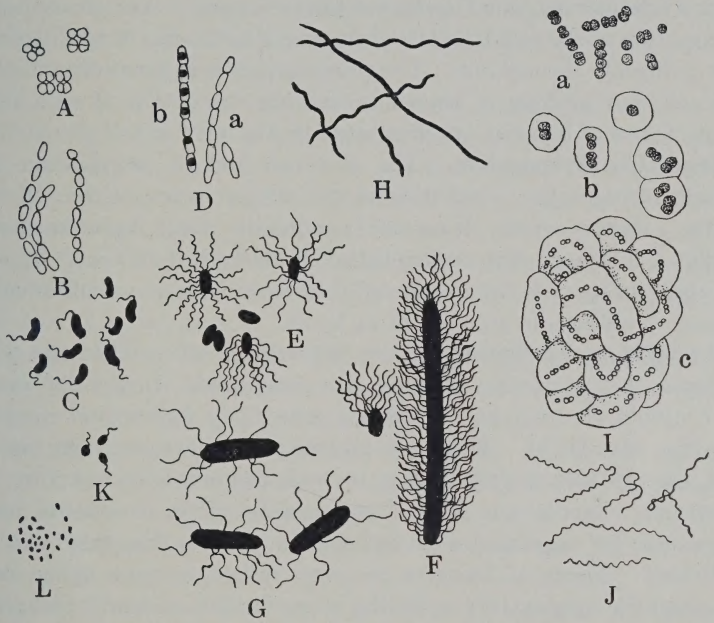


FIG. 181.—Various kinds of bacteria. A, *Micrococcus scarlatinus* Mig.; B, *Bacterium aceti* (Kütz.) Zopf., acetic acid bacterium; C, *Microspira comma* (Koch) Schröter, cholera bacterium; D, *Bacillus anthracis* Koch, × 1500; E, *Bacillus typhosus* Eberth, typhoid bacterium; F, *Bacillus vulgaris* (Hauser) Mig.; G, *Bacillus subtilis* (Ehrenb.) Cohn, hay bacillus; H, *Spirillum tenue* Ehrenb.; I, *Leuconostoc mesenterioides* Cienk. (*Streptococcus mesenterioides* (Cienk.) Mig.); *a*, in sugar free culture; cells not surrounded by a gelatinous substance; *b*, cells surrounded by gelatinous substance; grown in sugar-containing medium; *c*, older gelatinous mass; J, *Spirochaete obermaieri* Cohn; K, *Nitrosomonas europea* (*Winogradsky*) Mig., nitrate bacterium; L, Nitrobacter. All except D, × 1000. (A, after Migula; B, C, E, F, G, H, J, from Engler and Prantl; D, I, K, L, after A. Fischer.)

are motile in certain stages of their life-history and non-motile in other stages. Spores are never motile. Several forms of bacteria are shown in Fig. 181.

Bacteria live as isolated cells or in the form of films or masses, known as *zoögloea*. One of the most remarkable zoögloea-forming species is *Leuconostoc mesenterioides* (Cienkowsky) Van Tieghem, which gives rise to the large gelatinous masses formerly known as "frog-spawn" or "gomme du sucrérie" in European sugar factories. The plant consists of Nostoc-

like colonies of rounded cells embedded in a gelatinous substance (Fig. 181, I, *c*). The individual colonies form rounded or elongated masses of about two cubic centimeters in volume, but so rapid is growth under favorable conditions that a volume of 4900 liters of 10% sugar solution may be converted into a gelatinous mass in 24 hours.

Each cell is provided with a definite cell wall, which in rare instances shows a cellulose reaction (*Bacterium pasteurianum*). As regards the internal structure of the cell little is known, owing to the fact that the contents stain uniformly throughout. The presumption is in favor of a nucleus in each cell, but nothing is known concerning the details of such a body. Several forms of bacteria are illustrated in Fig. 181, A-J.

Vegetative Propagation.—The chief method of propagation in all bacteria is vegetative, consisting of the simple fission of the cell at the middle. Under certain favorable conditions many bacteria multiply rapidly, a division being accomplished in about half an hour. It will be seen that, under such circumstances, the descendants of an individual may amount to millions in a period of 24 hours.

Propagation by Spores.—Some bacteria produce what are known as spores, and two forms of spores are recognized. In the one case the cell contents contract and develop a new thick wall within the parent cell (Fig. 181, D, *b*). These are internal, or *endospores*. On the other hand, the cell may merely thicken its wall, forming what is known as an *arthrospore*. Spores are formed presumably when conditions become unfavorable for vegetative activity, and the plant is thus tided over such conditions. Spores of bacteria are very resistant, some being able to withstand the temperature of boiling water for half an hour or longer.

Distribution.—Bacteria occur in every region of the earth that is capable of sustaining life of any kind. Many live within the tissues of plants and animals, where their presence may produce the abnormal condition known as disease. Although most bacteria require the oxygen of the air (aerobic bacteria), many, like those that live in the mud under water or at the bottom of a pond, and those causing such diseases as tetanus (lockjaw), thrive in the absence of oxygen. In fact, some are unable to develop in the presence of air; such bacteria are said to be *anaerobic*.

Bacteria in the Economy of Nature and of Man.—Inasmuch as many bacteria are harmful to plants, lower animals, and man, there is a widely-prevailing popular notion that all bacteria are injurious. But, as a matter of fact, many of these small plants are among the most useful and necessary organisms. If all bacteria were to perish from the earth, the balance in nature would be so upset that the result cannot be imagined. In past ages these plants played a part in the formation of various

geological deposits. In the soil their activity is such that, though at present very imperfectly understood, doubtless many higher plants could not thrive if bacteria were absent. By their activities (fermentation and decay) the waste products and dead bodies of plants and animals are converted into the elementary compounds out of which these plants and animals were composed. Bacteria not only contribute to the renewal of the soil, but also render it suitable for use by higher plants. Certain bacterial fermentations are the means by which many foods are produced for the use of man and animals.

Let us now turn our attention to a few of the kinds of bacterial activity.

Nitrifying Bacteria.—Certain bacteria living in the soil, though devoid of chlorophyll, secure their food from purely inorganic material. One of these (Nitrosomonas) oxidizes ammonia to nitrous acid. Another (Nitrobacter) oxidizes nitrous acid to nitric acid. Nitric acid thus produced may then combine with other substances in the soil, forming soluble nitrates useful to plants. The work done by these bacteria is referred to as *chemosynthesis*.

Nitrogen-fixing Bacteria.—The tubercle bacteria which are found in the soil and which live in connection with the roots of leguminous plants have been commented upon in the chapter on roots.

Iron Bacteria.—A few bacteria (*Cladothrix dichotoma*, *Leptothrix ochracea* Kuntzig, *Spirophyllum ferrugineum* Ellis, *Gallionella ferruginea* Ehren.) are able to utilize iron salts, and, as a result, iron oxide is deposited in a sheath formed by the cell wall. The surface of water may sometimes appear rusty red, owing to the presence of these bacteria.

Sulphur Bacteria.—Bacteria that utilize compounds of sulphur are more abundant than iron bacteria. They oxidize hydrogen sulphide, the sulphur being set free in the form of granules in the cell. Some sulphur bacteria are colorless (*Beggiatoa alba*), while certain others (*Cromatium weissii*, *Thiocystis violacea*) possess a violet or purplish pigment, *bacteriopurpurin*.

Sulphur and iron bacteria have doubtless played an important role in past ages in the formation of such geological deposits as kaolin. There is also some evidence to indicate that certain bacteria as *Micrococcus silenicus* Brenner, which occur in mud or ooze under water, are capable of oxidizing silenium, although that fact has not as yet been definitely established. Such bacteria are sometimes regarded as representing a more primitive type of organism in which metabolism is simpler. It would seem probable that a number of exothermic reactions which take place in ooze play a role in the maintainance of life in such organisms.

Bacteria which secure their sustenance or energy largely from inorganic matters are said to be *autotrophic*.

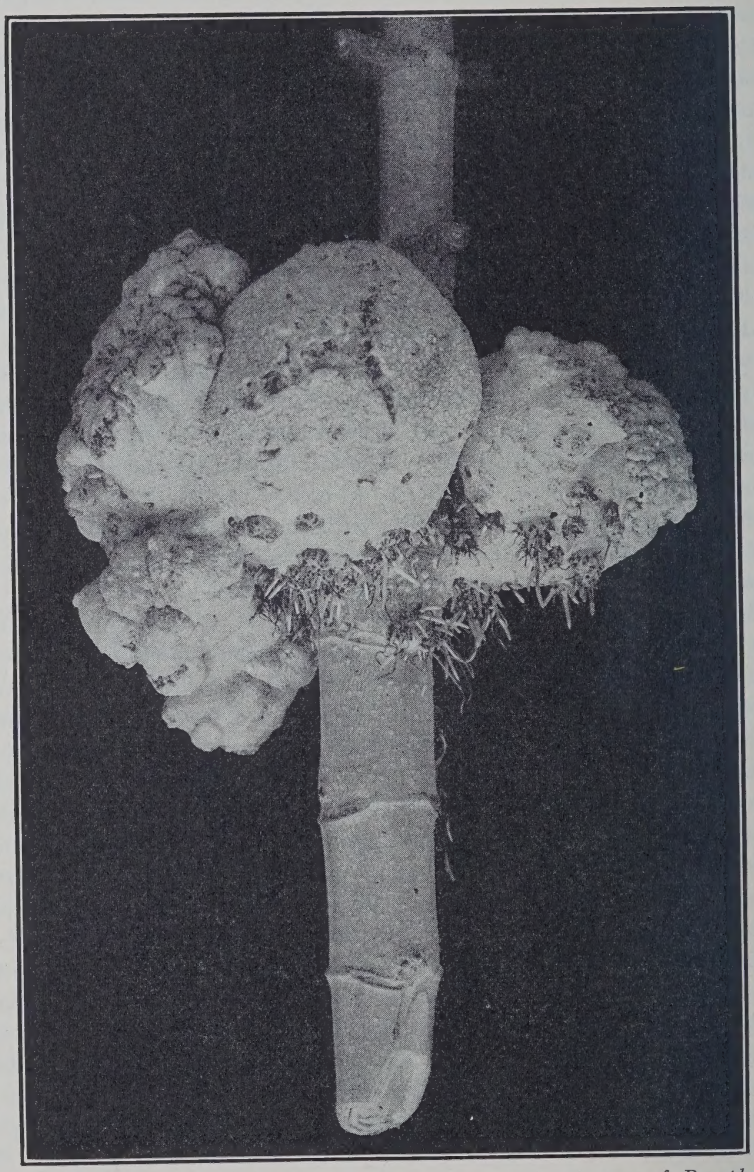


FIG. 182.—Crown gall or tumor-like proliferations of the stem of *Bryophyllum calycinum* inoculated with *Bacterium tumefaciens* (hop strain). Photo. by the late Erwin F. Smith.

Pathogenic, or Disease-producing, Bacteria.—We shall here call attention to a few bacterial diseases of plants only. All of our knowledge of bacterial diseases of plants began about 40 years ago, when T. J. Burrill demonstrated that the common fire-blight of pear, apple, and quince was caused by the parasite, *Bacillus amylovorus* (T. J. Burrill) Trevision. Sixteen years later Erwin F. Smith ventured the statement that "there are probably as many bacterial diseases of plants as of animals," and more recently the same author offered an even broader generalization, namely, that in all probability it will be found that bacterial diseases occur in every family of plants.

In the body or cells of the host, the bacteria produce poisons (toxins) which may kill or disorganize the cells. The whole plant may be affected, or the effect may be local and confined to some particular part.

The fire-blight of apples, pears, and quinces kills young shoots and sometimes the larger branches, causing the leaves to turn brown as if scorched by fire. Infection is brought about by bees and other nectar-sipping insects, which carry the bacteria from "hold-over blight" or "cankers" of previously diseased trees to the flowers, where the organism begins its growth in the nectaries. From the blossoms it passes down, mainly through the bark, into the larger branches of the tree. The destruction of the cells of the inner bark girdles the branch and causes its death.

Crown gall, plant cancer, is due to the parasite, *Bacterium tumefaciens* Smith and Townsend. The presence of this organism in the host tissue results in an overgrowth of the affected part (Fig. 182). This, usually large, tumor or knot-like growth often occurs on the trunks of fruit trees near the ground, that part known by gardeners as the "crown." The disease occurs on a great variety of cultivated plants, and upon some wild ones, such as the chestnut. The cells of the parts affected are not killed or destroyed, but are stimulated to abnormal growth and division, the result being a gall that may be larger than the root or stem that bears it. In this behavior of the cells of the host, crown gall bears a striking resemblance to human cancer. The largest galls develop from the cambium, but smaller ones may be formed from the bast and cortex. Fruit trees may live and bear fruit several years after the noticeable presence of the gall.

Cucurbit, or Cucumber, Wilt is caused by *Bacillus tracheiphilus* E.F.S. It occurs upon various members of the cucumber family, but it is not known outside of this family. The bacteria grow inside the conducting vessels of the xylem, producing a slime or mucilage that plugs the vessels. This prevents the passage of sufficient water to the leaves, thereby causing them to wilt. The leaves wilt suddenly, and without apparent cause,

and the whole plant dies in a short time. Infection is spread by certain insects that feed upon the plants.

Brown Rot of the Solanaceae results in the wilting and rotting of leaves and stems. It is caused by *Bacterium solanacearum* E.F.S. It occurs on potato, tomato, egg plant, and other members of the nightshade family, as well as upon species of the nettle and bean families.

Among other common bacterial diseases are the black rot, or "black leg," of potato, due to *Bacillus phytophthorus* Otto Appel; the bean blight caused by *Bacterium phaseoli* E.F.S.; mulberry blight caused by *Bacterium mori* Bayer and Lambert emend. E.F.S.; and others too numerous to mention here.

Bacterial parasites act variously upon the plant. Sometimes the plant as a whole is affected, resulting in an early death; or the disease may be confined to certain circumscribed portions. On the other hand, parasitic bacteria may produce no injury to the plant as a whole, but may be even beneficial, as in the case of the tubercle bacteria of the legumes, where the relation is regarded as one of mutual symbiosis. One of the most remarkable cases of mutualism is found in the tropical East Indian Ardisia, a hothouse plant grown for its ornamental red berries and evergreen foliage. The bacteria are most abundant in the leaf teeth, where they form pockets or cavities, making the teeth appear yellow and swollen, but never causing the leaves to die or fall. Plants grown from seeds in the absence of bacteria remain very small and stunted. It would thus seem that Ardisia requires the bacteria.

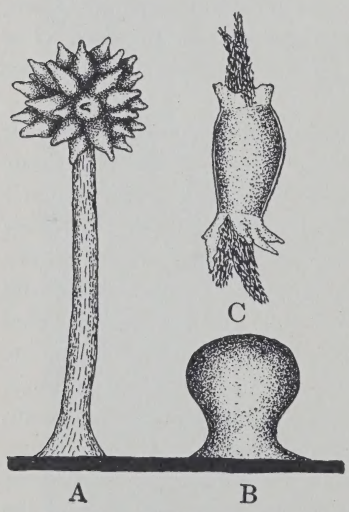


FIG. 183.—*Chondromyces apiculatus* Thaxter. A, cystophore with cysts in different stages of development; B, young cystophore; C, cyst germinating. On dung of antelope from Liberia, Africa. (After Thaxter.)

MYXOBACTERIACEAE

The Myxobacteriaceae consist of bacteria-like cells held together by a slimy or mucilaginous substance which they secrete, thus forming a pseudo-plasmodium that bears some resemblance to the plasmodium of the slime moulds. It differs from the latter, however, in that the cells do not fuse. The cells bear a close resemblance to round or rod-shaped bacteria, and exhibit a slow, creeping movement. After the vegetative period, which, in artificial cultures, may last a week or two, very definitely shaped and bright-colored fructifications

are produced in some species, as shown in Fig. 183, A. Here we have a little column or stalk, at the top of which are formed the pear-shaped cysts (sporangia) containing the spores. The wall of both cyst and stalk is formed from the hardened mucilaginous material. The germinating cysts give rise to new pseudoplasmodia (Fig. 183, C). Nearly all the members of this group lives saprophytically upon the dung of animals. Almost our entire knowledge of this interesting group of plants is due to the researches of Thaxter.

CHAPTER XI

THALLOPHYTA—ZYGOPHYCEAE

The Zygophyceae are mainly one-celled plants of a yellowish or yellowish-green color, which may live as single cells or the cells may be held together by means of a gelatinous substance or they may remain attached end to end following cell division. In reproduction by cell union the cells become joined together directly and without undergoing any change in form or with but a slight change in shape. Representatives of the two classes, Conjugales and Bacillariales, will be discussed here.

CONJUGALES. POND OR WATER SILKS, DESMIDS

The Conjugales include those algae commonly known as pond silks or water silks. They occur only in fresh water. The individual plants are either single cells or filaments. They are recognized by the characteristic chloroplasts, which may be in the form of a band, or a number of bands, spirally arranged in the cell, a flat plate, or a star-shaped body.

As an introduction to the study of the green algae we may select as a concrete illustration the very familiar Spirogyra, inasmuch as some first-hand knowledge of the plant may be acquired by the beginner in his laboratory exercises.

Spirogyra (Pond Silk).—Spirogyra is common in fresh water ponds and streams. It is slippery to the touch and usually forms floating masses or scums. It may live also entirely under water attached to earth, stones, and other objects.

Structure.—In structure Spirogyra is an unbranched filament consisting of a single row of cylindrical cells placed end to end. The slime secreted by the cells gives the filaments their slippery feel. Each cell may contain one or more band-like chloroplasts—the number depending upon the species—arranged spirally in the cell (Fig. 184, A). The chloroplasts have usually irregular or scalloped edges, and they may be trough-shaped rather than flat. Spaced at regular intervals in the chloroplasts are conspicuous objects, *pyrenoids*, which are centers for the formation of starch (Fig. 184, A). The bulk of the cytoplasm in the cell is spread over the inner surface of the wall in a very thin layer in which the spiral chloroplasts are held. The center of the cell is occupied by a large vacuole filled with cell sap. In this, the nucleus is suspended in a mass of cyto-

plasm, from which radiate strands of cytoplasm that end near the pyrenoids or in the wall layer of cytoplasm, (Fig. 184, A).

The cell wall is thin and colorless. Upon it is produced externally the mucilaginous slime. In some species the end walls of the cells possess characteristic infoldings.

Vegetative Reproduction.—The cells of Spirogyra multiply by transverse division. Normally cell division occurs at night, beginning about nine o'clock or later. To observe the division in daylight, it is necessary to inhibit the process by keeping the plants in a refrigerator from the

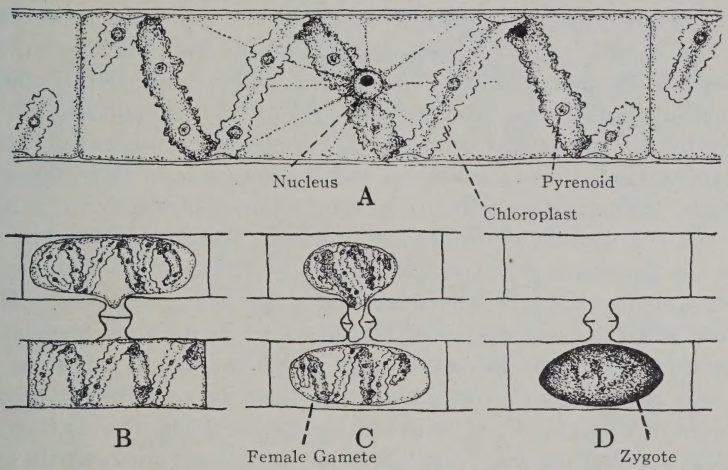


FIG. 184.—Spirogyra. A, a vegetative cell; B, C, D, formation of zygote.

time the division is about to begin (9:00 p. m.) until the time of observation on the following day.

Under certain environmental conditions the filaments may break into two or more pieces, and each piece by growth and division of its cells may develop into a long filament. When filaments are transferred from their normal habitat out of doors to a vessel in the laboratory, the cells tend to separate from each other, many of them dying. The parts which remain alive may grow into new filaments after a time, thus re-stocking the vessel.

Occasionally the contents of certain cells will round up to form cells resembling spores, which are termed *aplanospores*.

The filaments of Spirogyra are now generally regarded as colonies, each cell being an individual, inasmuch as the cells are totipotent.

Reproduction by Gametic Union, Sexual Reproduction.—In the foregoing we learned that new filaments, i.e., new plants, may arise from *one*

parent cell. Spirogyra and the vast majority of plants reproduce also in another manner in which *two* parent cells take part. The two germ cells, involved in the process are called *gametes*. A *gamete* is a reproductive cell which cannot by itself grow into a new plant; it must unite with another gamete of a different kind. The cell resulting from the union of two gametes is capable of producing one plant in Spirogyra, but in some other algae it may give rise to two or more plants.

In certain species of Spirogyra the process is as follows: two filaments, or parts of filaments, parallel each other, often becoming twisted about one another if they are of considerable length. The cells of the two filaments which are opposite send out short protuberances which meet end to end, and a conjugating canal results from the dissolution of the walls at the point of contact (Fig. 184). This dissolution is effected by a cellulose-dissolving enzyme produced by the protoplasm. In the cells of the filaments which will eventually unite, the contents will become self-plasmolyzed, thus rounding up and separating from their respective cell walls. (Plasmolysis refers to the contraction of the cell contents away from the cell wall owing to the loss of water. When this happens normally the process is called self-plasmolysis.) In one of the filaments the contents of the cells will remain in their respective cell cavities. These cells are called the receiving cells (Fig. 184, C). In the other filament the protoplasts of the cells will not remain within the parent cell walls, but they will move through the conjugating tubes into the receiving cells, as shown in Fig. 184, C, D, where the contents of any two uniting cells will fuse, forming one cell. In this union, cytoplasm mingles with cytoplasm and the two nuclei place themselves side by side and fuse into one. The cell whose protoplast passed over into the receiving cell is termed the supplying cell. The contents of the supplying cells usually round up before the plasmolysis of their receiving mates (Fig. 184, B). The passage of the protoplast of the supplying cell through the conjugating tube into the receiving cell and the union of the two protoplasts is accomplished by the activity of contractile vacuoles present in the protoplasts.

The protoplasts of the two cells which thus unite are *gametes*, and the cell formed by their union is the *zygote*. The zygote develops a firm cell wall of three layers, and passes into a dormant condition, or resting stage. The zygotes may remain viable for some time in a dry state. The zygote is the dry land condition of the otherwise aquatic plant.

In some species, neighboring cells of the same filament conjugate to produce zygotes.

The Germination of the Zygote.—When growth is resumed the zygote absorbs water, swells up and bursts the two outer layers of the zygote wall. The contents with the inner layer as its wall emerges as an elongated cell

(Fig. 185, G, H). The cell now divides transversely into two cells. The more slender basal cell becomes the holdfast in case the plant is attached to some support, while the terminal cell divides. The two resulting cells continue growth and division, and the result is a new filament of many cells.

The species of Spirogyra shown in Fig. 184 has but one chloroplast, one spiral band, in each cell. It is evident that the zygote contained two, one from each gamete. When the zygote germinated the new plant had only one chloroplast in each cell instead of two. What happened to the

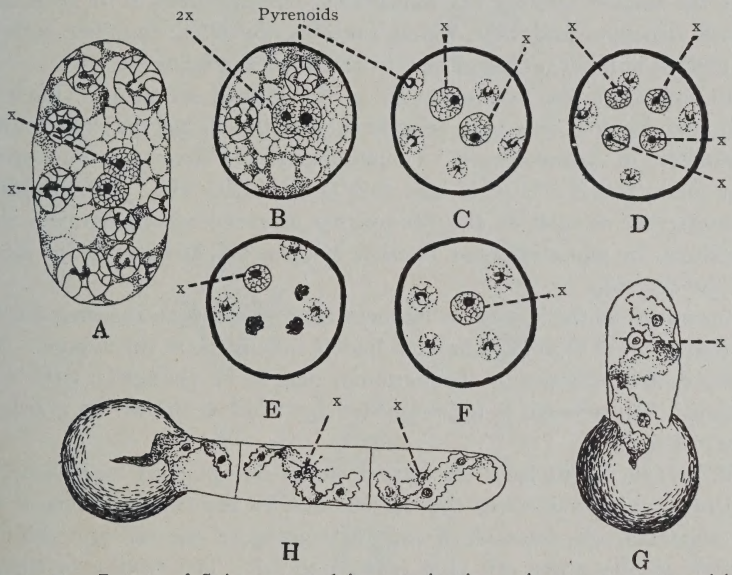


FIG. 185.—Zygote of Spirogyra and its germination. A, young zygote with the two gamete nuclei in contact; B, nuclei united; C to F, internal steps in the process of germination. C, after first nuclear division; D, after second nuclear division; E, three of the four nuclei disintegrating; F, zygote just before bursting of cell wall. G, H, filaments developing from zygote; *X* single or haploid number of chromosomes; 2*X* double or diploid number of chromosomes. (A, B, from Mottier, Fecundation in Plants; D to H, diagramatic.)

chloroplasts? We do not know definitely. One supposition is that one of them, presumably that of the supplying cell, disintegrates, while the other continues and gives rise to the chloroplasts of the new plant (Fig. 185, H).

The Meaning of Reproduction by the Union of Gametes.—In the union of the gametes the most important thing is the fusion of the two nuclei (Fig. 185, A, B). In the chapter on the cell (Chapter II) we learned that the nucleus as it divided revealed a definite number of chromosomes (see Fig. 13). During the division of the nucleus each chromosome splits

lengthwise and all the new cells have the same number of chromosomes. The chromosomes are regarded as the principal bearers of the hereditary characteristics of a living organism. By heredity we mean *that something* which determines that a bean will produce a bean plant; a grain of corn, a corn plant, and an acorn, an oak tree.

A plant which comes from one parent cell has but the heritage of one parent, while the zygote has a double heritage. The zygote has, therefore, twice as many chromosomes as that possessed by each gamete. In every organism which reproduces by gametic union, the structure which contains the double number (2x number) of chromosomes in its cells, is the *diploid structure*, and that which contains the single number (one-half the diploid number, or x-number) is the *haploid structure*.

In Spirogyra the young zygote is the diploid structure. Each filament is an haploid structure because each of its cells has the single number (x-number) of chromosomes. Consequently, the filament which springs from the zygote is a haploid structure (Fig. 185, G, H). The life-history of Spirogyra, as well as the life-history of every other organism which reproduces by gametic union, consists of these two structures, the *haploid* and the *diploid*.

Inasmuch as the Spirogyra filament coming from the zygote is haploid, the change from diploid to haploid had to take place in the zygote. That is, the double number of chromosomes had to be changed to the single number. The change is accomplished by what is known as a *reducing nuclear division*.

In a reducing division the chromosomes do not split lengthwise, but they form pairs, and when the nucleus divides the two members of each pair separate, one member of each pair going to one cell and the other member to the other cell (Fig. 185, A to E). The *number* of chromosomes in each cell is consequently reduced to one-half. With the aid of Fig. 186, we shall see what happens to the chromosomes during a reduction division of the nucleus. Let it be understood that the illustrations of this figure are merely diagrams of a few stages of the process; they are not pictures of the actual steps that would be seen in Spirogyra or in any other plant.

In the reduction division a spirem is formed as in the case of an equational division. Fig. 186, A corresponds to the stage of the spirem, which represents all the chromosomes united end to end. In this case there are six, but the limits of any chromosome in the spirem are not recognizable. The spirem now segments into the six chromosomes, which tend to be arranged in pairs, as in B. The three pairs are next arranged on the spindle, as in C. Now, one member of each pair passes to one pole of the spindle, and the other member to the other pole, as in D. Each

daughter nucleus (E) thus formed receives three chromosomes of the six, or just one-half the number possessed by the parent nucleus. The nuclei of these two cells are, therefore, haploid nuclei.

In the germination of the zygote those changes which we observe externally are shown in Fig. 185, G, H. The internal changes are indicated in C, D, E, F. They cannot be seen directly, but only from stained sections made at the proper stages in the process. These internal changes

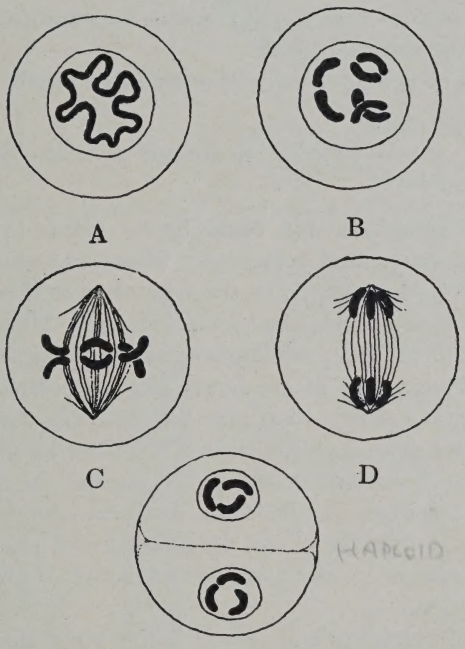


FIG. 186.—Diagrams illustrating a reducing nuclear division. A, the hollow spirem. B, spirem has segmented crosswise into the chromosomes which have approximated in pairs. C, pairs of chromosomes arranged in the equator of the spindle. D, one of each pair, or one-half the whole number, has reached the pole of the spindle. E, daughter nuclei, each with the reduced number of chromosomes.

are as follows: the zygote nucleus undergoes the reducing division, and each of the two nuclei in Fig. 185, C, has the single (x) number of chromosomes; these two nuclei divide equationally to produce four nuclei. Of the four, three disintegrate, leaving one (Fig. 185, F) in the cell which becomes the starting point of the new haploid structure.

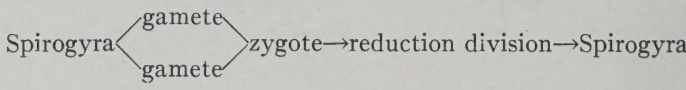
Let us bear in mind that there can be but one reducing division in a life cycle, as there is but one union of gametes or one doubling of the number of chromosomes in a life cycle. All other nuclear divisions in

the life cycle in both haploid and diploid structures,—and there may be millions of them,—must be equational.

The significance of gametic union consists in the creation of the diploid structure. This structure has made possible the evolution of the highest organisms, for, the largest and most important structure of the highest plants and animals is the diploid structure.

As we proceed in our study of the different groups of plants from the simpler to the highest, we shall find that the haploid and diploid structures differ in various ways as regards relative size, appearance, and physiological dependence one upon the other.

The life cycle of Spirogyra may be represented briefly thus:



Hydrophyte, Xerophyte, and Mesophyte.—Plants that live in water or in marshy places are called *hydrophytes*, when mentioned with reference to their physical environment. In the vegetative condition then, Spirogyra would be a hydrophyte, or an aquatic plant. Plants such as cacti, that may live where there is a minimum of water, as in a desert, are known as *xerophytes*. Plants such as our forest trees of beech and maple, and the ordinary flowers and ferns that grow among them, as well as ordinary crops, requiring intermediate conditions of moisture supply and drainage, are called *mesophytes*, or middle plants. A mesophyte or a hydrophyte may take on a *xerophytic condition* and exist with only a very limited water supply, as in the case of our deciduous forest trees in winter. A beech tree, for example, is not a xerophyte, but in the winter it is in a xerophytic condition.

The zygote of Spirogyra will remain viable when the pond dries up, and the bottom of a dried-up pond represents a xerophytic environment in so far as Spirogyra is concerned. The zygote is therefore, the dry land stage of the otherwise aquatic plant. It is thus seen that it is the zygote in Spirogyra that enables the plant to tide over conditions unfavorable or unfit for its vegetative development.

Zygnemaceae, Pond Silks.—In our flora the majority of the Conjugales belong to the families, Zygnemaceae and Desmidiaceae, or Desmids. Of the Zygnemaceae the genera most commonly met with are Spirogyra, Zygnema, and Mougeotia (Mesocarpus). All of these consist of unbranched filaments. In Zygnema there are two star-shaped chloroplasts in each cell, while the cells of Mougeotia contain each a long chloroplast that appears as a straight, flat band, or it may have a twist at the middle. All of these plants when not attached to objects below the sur-

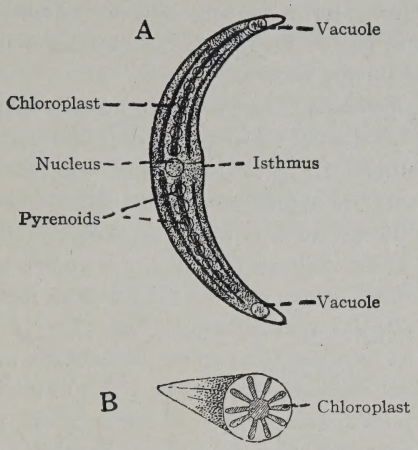


FIG. 187.—A, a desmid, Closterium. B, cross section, showing star-shaped chloroplast.

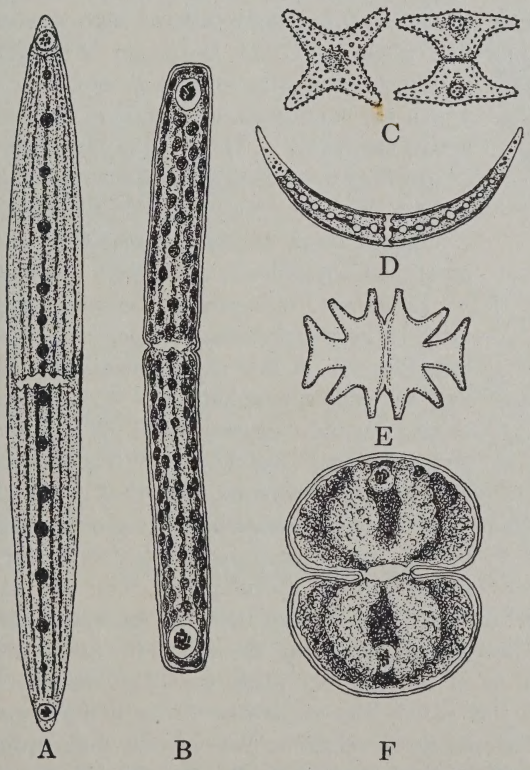


FIG. 188.—Some common Desmids. A, D, Closterium; B, Docidium; C, end and side views of Staurastrum; E, Micrasterias; F, Cosmarium. (E, after Wolle.)

face of the water may form floating masses, which are buoyed up by entangled bubbles of gas derived from the process of photosynthesis and the expansion of air in the water.

Desmidiaceae, Desmids.—Desmids are unicellular plants that live as isolated cells, or the cells may adhere to form filaments. The numerous species are all confined to fresh water. Many are objects of beauty because of their form and symmetry. Most desmids consist of two symmetrical halves with the nucleus near the center of the cell (Fig. 187). The middle part of the cell is known as the isthmus. In some forms, such as Cosmarium, the cell is deeply constricted at the isthmus (Fig. 188, F). The chloroplasts, as in other Conjugales, are always in the form of some definite pattern, one or two to each cell. The chloroplasts may be star-shaped, lobed, or in the form of flattened, radiating plates united in the axis of the cell (Fig. 187, B). One or more conspicuous pyrenoids are present in the chloroplasts of some species. In forms like Closterium and Docidium (Fig. 188, A, B, D) a vacuole is usually present in each end of the cell, in which are seen minute crystals of sulphate of lime in active movement. This kind of movement is known as a Brownian movement, named in honor of the discoverer, Robert Brown.* Fig. 188, A-F, represents some of the commoner forms of desmids met with among the filamentous Conjugales or along with other algae.

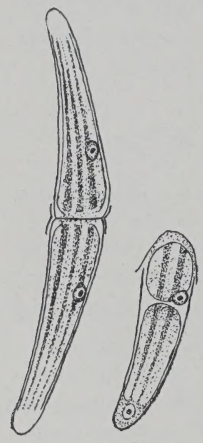


FIG. 189.—Vegetative propagation in the Desmid, Closterium. A, the cell has just divided; B, one of the old half-cells regenerating a new half. The chloroplast of the old half-cell has divided, and the nucleus is taking position between the two plastids. (After A. Fischer.)

Vegetative Propagation.—Desmids propagate vegetatively by a transverse division at the middle of the cell (Fig. 189, A, B). After the division of the cell each half develops a new half-cell. Consequently, each resulting desmid consists of one old half and a newly regenerated half (Fig. 189, B). The chloroplast for the new half-cell grows out from that in the old half-cell.

Sexual Reproduction.—The process of the formation of the zygote may be illustrated in the well known Closterium or Cosmarium. The two cells approach each other and are held together by the mucilaginous slime. Each cell sends out a protuberance. These meet end-to-end and form a conjugating canal as in the case of Spirogyra. The two protoplasts, however, meet in this canal, and there fuse to form the zygote (Fig. 190, A to C). The zygote develops a heavy wall with projecting spines, and passes into a stage of dormancy (Fig. 190, D).

* Discovery reported in 1827.

Germinaton of the Zygote.—According to Klebahn the gamete nuclei do not fuse until the beginning of the germination of the zygote (Fig. 191, A, B). As germination proceeds there occur two successive nuclear divisions, and the cell may also divide, so that each daughter cell will contain two nuclei, one of which will disorganize (Fig. 191, C, D, E). In this desmid, therefore, two individuals result directly from the zygote. The concluding steps in the process are shown in Fig. 191, E, F. It is highly probable that the first mitosis following fusion in the zygote is a

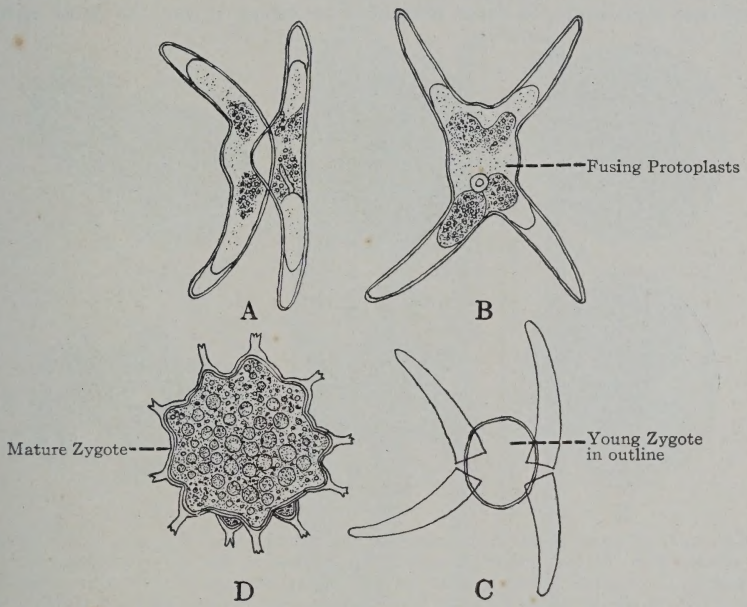


FIG. 190.—Formation of zygote in Desmids. A, two cells of Closterium coming together; B, the protoplasts fusing; C, the zygote formed, contents not shown. D, mature zygote of *Cosmarium botrytis* Menegh., showing spiny processes of the wall. (A, B, D, after DeBary; C, from "A Treatise on the British Freshwater Algae," by the late G. S. West; revised by F. E. Fritsch. Cambridge University Press, 1927.)

reducing division. The zygote, therefore, represents the diploid structure, while the individual desmid cells constitute the haploid structure.

BACILLARIALES—DIATOMS

Diatoms are unicellular plants varying greatly in form and size. All possess a characteristic structure due to the fact that the cell wall consists of two parts (valves), one fitting over the other like the two parts of a box (Fig. 192, B). The cell wall is strongly impregnated with silica, which is variously marked by rows of minute pores. When all organic matter is removed from the cell, the remaining siliceous shell or skeleton presents the original shape of the diatom and reveals the characteristic markings.

Because of these markings, many diatom shells are among the most beautiful objects of the microscopic world.

Diatoms are widely distributed over the surface of the earth, occurring on damp ground, on stones in moist places, and in bodies of both fresh and salt water, where they may constitute a very important element of the floating life known as *plankton*. They are sometimes so numerous as to impart a characteristic color to the water in which they are suspended.

Diatoms occur as isolated cells, or they may adhere, by means of a gelatinous substance, to form filaments or zigzag rows. In some species

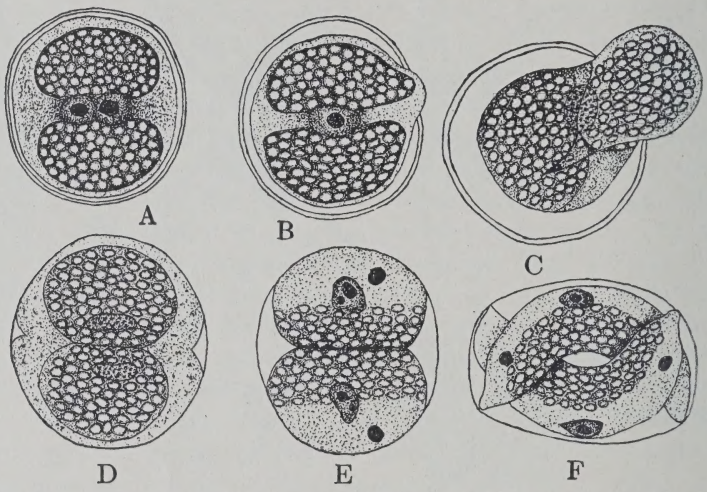


FIG. 191.—Fusion of nuclei of gametes and germination of zygote in Closterium. A, gametes with the two nuclei in contact; B, the nuclei have united and germination has begun; C, contents escaping from old wall of zygote; fusion nucleus in prophase of division; D, daughter nuclei formed; E, second nuclear division and cell division completed. In each daughter cell, one of the two nuclei is much smaller and denser; these small nuclei will disorganize. F, the daughter cells have begun to assume the form of the adult desmids; the degenerating nuclei lie in the ends of their respective cells. (After Klebahn.)

the cells are enclosed in gelatinous tubes; in others the cells develop gelatinous stalks, by which they are fastened to objects in the water, forming colonies (Fig. 193, A, E). The gelatinous substance is produced by the protoplast and exuded through pores in the cell wall.

Structure of the Cell.—As an illustration of cell structure we shall select some large form like Pinnularia or Navicula (Fig. 194, A, B). As stated, the cell wall consists of two halves, or *valves*, one fitting into the other like a box and its overlapping lid. In many diatoms the two halves are symmetrical, but in others they are not. Each valve consists of two parts, the top and the margin, or *girdle*. The top corresponds to the top or the bottom of the box, and the girdle to the overlapping sides of the

box and its lid. The cell is described as seen from the valve view and from the girdle view.

In the valve view of Pinnularia or Navicula (Fig. 192, A) markings are seen extending from the margin toward, but not reaching, the center. The central smooth place shows at its middle and at each end, strongly refractive spots, the *nodules* (Fig. 192, A). From each end nodule a line extends to the middle nodule. This line, the *raphe*, is a cleft or series of

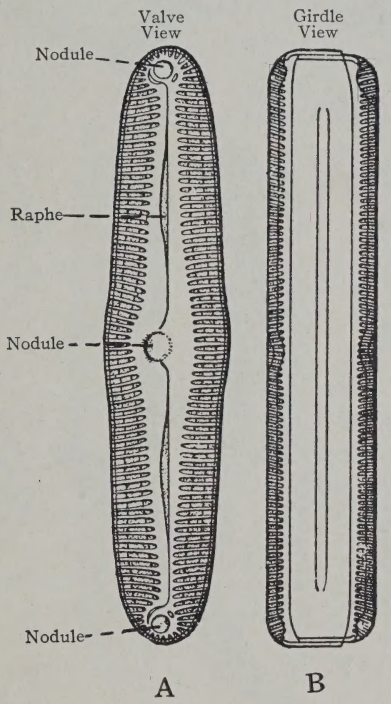


FIG. 192.—Two views of the shell of Pinnularia. A, valve view; B, girdle view. Note that one-half shell fits inside the other. (After Pfitzer.)

pores leading to the interior of the cell (Fig. 192, A). Through such openings as these the mucilage produced by the protoplast exudes.

The cytoplasm of the cell forms a wall layer with a bridge-like mass extending across the center, in which the nucleus lies. This bridge is best seen in the girdle view (Fig. 194, B).

Two chloroplasts are present in Pinnularia, in the form of large plates extending the length of the cell. In the girdle view (Fig. 194, B) they are seen from the flat side, while in the valve view their edges are turned toward the observer (Fig. 194, A). The chloroplast is of a golden brown or straw color. Its yellowish pigment is a mixture of chlorophyll and the

yellow pigment *carotin*, or *xanthophyll*. The pigment of the plastid is sometimes referred to as *diatomin*. In some species, Cocconeis, for example, there is but one chloroplast. In many the chloroplast is very irregular in form.

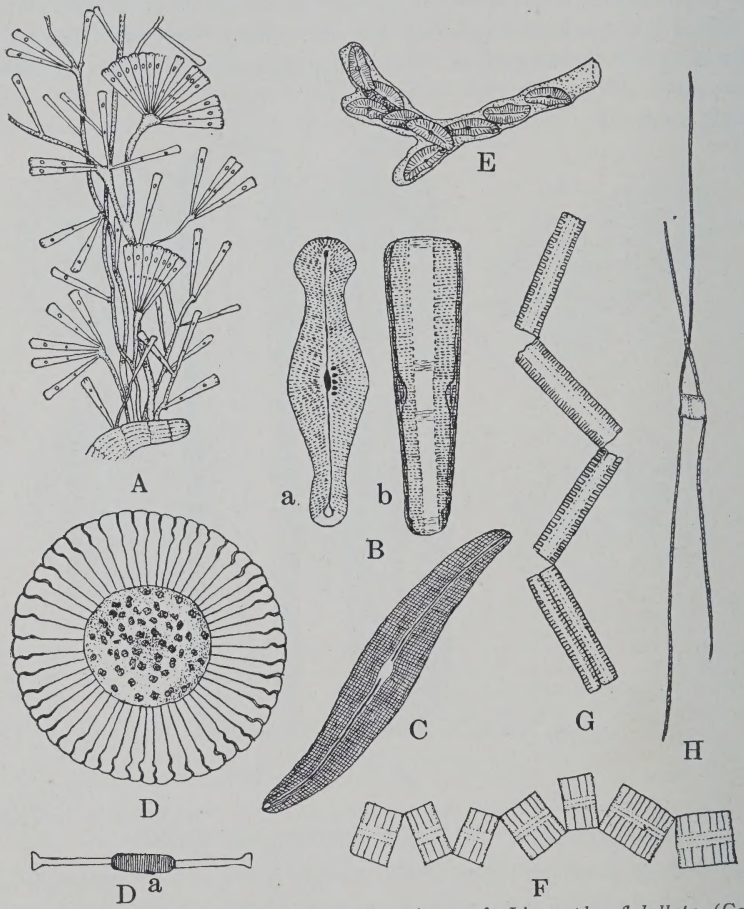


FIG. 193.—Some typical diatoms. A, colony of *Licmorpha flabellata* (Carm.) Ag : B, *Gomphonema geminata* (Lyngh.) Ag.; *a*, valve view; *b*, girdle view; C, *Pleurosigma attenuatum* (Kütz.) Wm. Sm.; D, *Planktoniella Sol* (Wallich.) Schutt.; a, valve view; E, *Cymbella caespitosa* Kütz.: F, *Tabellaria flocculosa* (Roth) Kütz.; G, *Diatoma vulgare* DeBary; H, *Chaetoceras boreale* Bail. (From Engler and Prantl.)

Reserve food material is present in the form of oil.

Vegetative Propagation, Cell Division.—When the cell is ready to divide, the protoplast increases in size, pushing the two valves apart until only the edges touch. Following the division of the nucleus and chloroplasts the cytoplasm divides, and the two cells lie within the old

one, the two new valves lying back to back (Fig. 195, A-D). C and D are cross sections of A and B respectively. Of the two diatoms thus formed, one is of the same size as the parent cell, but the other is smaller. After many such divisions, it is evident that a considerable reduction in the size of some of the individuals will result.

Vegetative Propagation and Rejuvenescence.—The diminution in size just mentioned is counteracted by a process of rejuvenescence, which may or may not result in cell multiplication. One of the simplest cases is illustrated by *Melosira varians* Ag. (Fig. 196, A-C). Here the protoplast

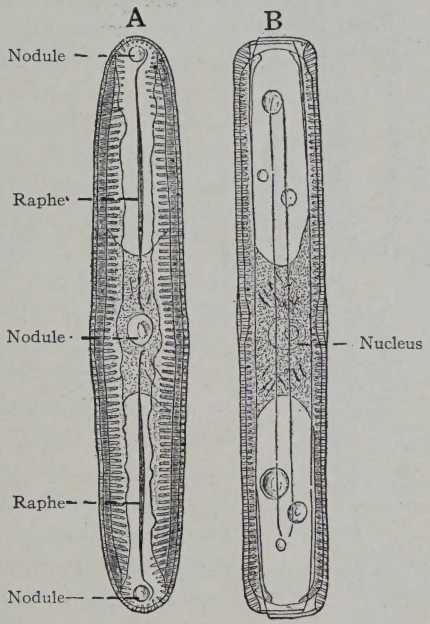


FIG. 194.—Two views of Pinnularia. A, valve, B, girdle, showing cell contents. (Strasburger, Macmillan Co.)

enlarges to two to four times the original size of the cell, forcing apart the valves. In this condition the cell has been called an *auxospore*, meaning "enlarging cell." This newly enlarged cell now develops a cell wall, and an enlarged diatom results. In some cases cell division accompanies auxospore formation, and there results cell multiplication as well as rejuvenescence.

Sexual Reproduction.—The formation of the zygote bears a close resemblance to that in the desmids. One of the simplest cases has been described by Karsten for *Cocconeis placentula* Ehr. The two cells come in contact, and the contents of each contract. The nucleus of each

has divided in the meantime, resulting in one large and one small nucleus (Fig. 197, A, B). During contraction each cell surrounds itself with a gelatinous envelope. Near the point of contact of the two individuals the halves of the cell separate somewhat. From the opening in one of the cells, which is regarded as the male gamete, a small papilla protrudes, which grows toward the opening in the female cell, and the gelatinous envelopes are soon in open communication. The entire contents of the male cell now pass through this narrow channel and unite with the female cell (Fig. 197, C, D, E). The two large nuclei eventually fuse, while the two small ones disappear (Fig. 197, F). The zygote increases in size and a new cell wall is formed. In the meantime the two chloroplasts are reduced to one. What has happened in the case of the chloroplasts?

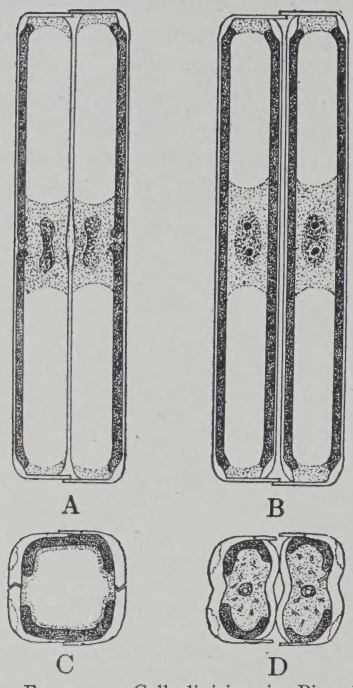


FIG. 195.—Cell division in Pinnularia. A, cell contents have enlarged and divided; the two half-shells have been pushed so far apart that the edges merely touch; the new half-shells have not yet been formed. C, a cross section of A. B, cell division is complete; each new half-shell fits inside an old one. D, cross section of B. (Figures adapted, A, B, after Lauterborn; C, D, after Engler and Prantl.)

A more complex process is shown in *Rhopalodia gibba* according to Klebahn (Fig. 198, A-D). The two individuals place themselves side by side, being held together by the gelatinous secretion. The protoplast of each undergoes rejuvenescence, and two successive nuclear divisions take place. Each cell now divides by constriction, and two nuclei pass to each daughter cell, one nucleus remaining functional, and the other disorganizing. Each individual diatom has thus produced two gametes (Fig. 198, A). The gametes of one individual now meet, by means of protuberances, with those of the other, and fuse. The functional nuclei also fuse (Fig. 198, C, D). The two zygotes soon assume the definitive form of the parent cells, and develop cell walls. The mucilaginous substance dissolves, and the new diatoms are set free.

It is clear from the foregoing that a zygote is very different from an auxospore, however much they may seem to resemble, and that the term *auxospore* should not be applied to the zygote.

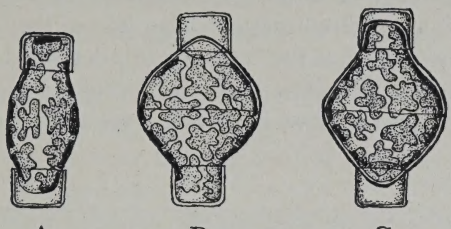


FIG. 196.—Auxospore formation in *Melosira varians* Ag. A, the halves of the shell have been pushed apart by the enlarging of the protoplast; B, C, the enlargement completed. These cells will develop new shells, and larger individuals will result. (Adapted from Engler and Prantl.)

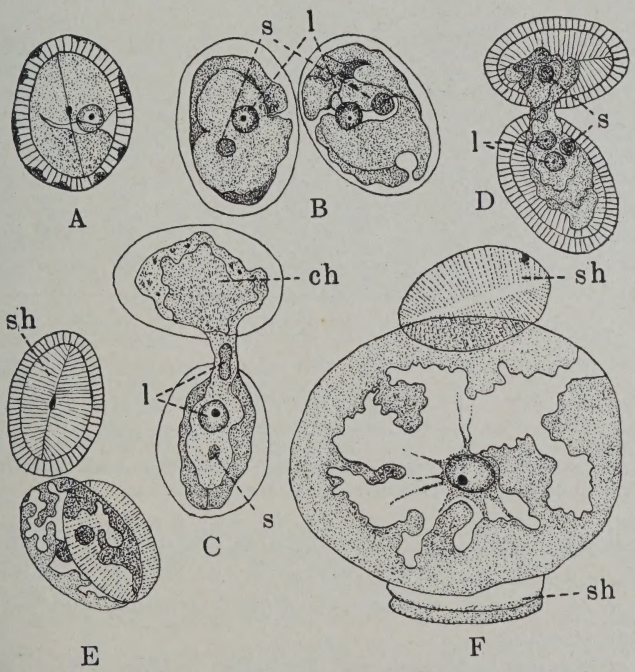


FIG. 197.—Formation of zygote in *Cocconeis placentula* Ehr. A, interior of cell, showing nucleus and one half of shell; B, two cells close together, the nucleus in each cell having divided, one of the daughter nuclei (*l*) being large, and the other (*s*) smaller; C, the protoplasts of the two cells have united; the large nucleus of the upper cell is in the narrow connection joining the two cells; D, the two large nuclei (*l*) lie side by side; the small nuclei (*s*) are degenerating, the two halves of the shell lie in position; E, the contents of the two cells have fused; F, the zygote has increased in size. *ch*, chromatophore; *sh*, empty shell. All figures ×1000. (Redrawn from Karsten.)

In the two processes of sexual reproduction just described rejuvenescence takes place, but multiplication occurs only in the latter case. The author is of the opinion that the "auxospore" described in the foregoing does not represent a degenerate process of reproduction, but a means of rejuvenescence, coupled in some cases with vegetative multiplication.

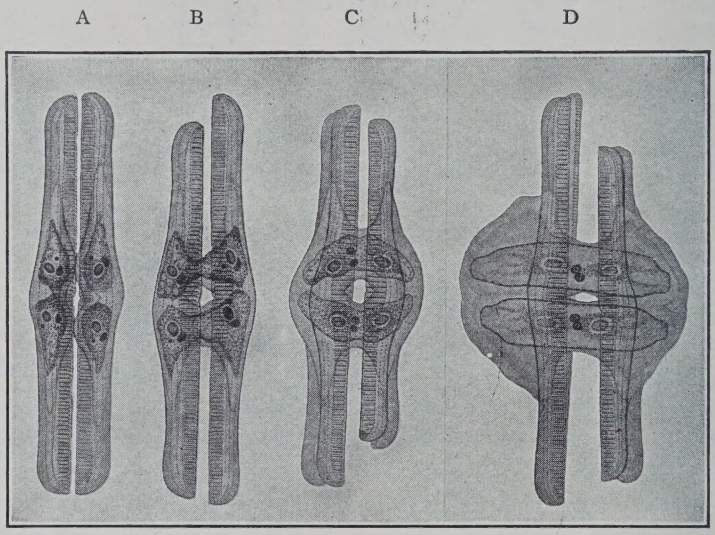


FIG. 198.—Formation of zygote in *Rhopalodia gibba*. A, conjugating pair seen from the valve side; protoplast of each has divided into two daughter cells, the gametes; each gamete contains, besides the large pyrenoid, a large and a small nucleus. B, cytoplasmic fusion of the two pairs of gametes has taken place; the small nuclei are scarcely recognizable. C, a later stage; the small nuclei have entirely disappeared, while the two functioning nuclei in each zygote, which has now changed from a dumbbell to an elongated form, have come nearer together. D, the two young zygotes have elongated and have begun to assume the adult form; gametic nuclei now in contact; cells surrounded by a gelatinous mass. (After Klebahn.)

If, during the nuclear divisions preceding the union of the gametes in Cocconeis and Rhopalodia, a reduction in the number of chromosomes takes place, the diatoms represent the diploid structure, and the gametes the haploid structure.

Role of Diatoms in Nature, and Their Use to Man.—Because of their great abundance at times, especially in the sea, and because of their direct importance as food for animals, and indirectly for man, diatoms have been styled "grasses of the sea." This fact may be illustrated as follows: small crustaceans, such as copepods, feed upon the diatoms; larger animals, such as herring, feed upon copepods, and still larger fishes feed upon herring, and some of these larger may be used as food by man. Their study as food for animals has been neglected until recently.

In past geologic ages the siliceous skeletons of diatoms formed extensive deposits known as "diatomaceous earth" or "kieselguhr." The extent of some such deposits give some idea of the great abundance of these plants existing at the time. While these deposits belong to comparatively recent geologic time, the plants may have existed at a much earlier period, but not in sufficient quantity to make their discovery certain. Diatomaceous earth has been used as an abrasive, as a base in the manufacture of dynamite, as a bacteriological filter, and in the manufacture of glass and porcelain. Because of their fine markings, the shells are used as test objects for microscope lenses. The beauty of the sculpturings of some shells entitles diatoms to the distinction of being spoken of as "jewels of the plant world."

Movement of Diatoms and Desmids.—Certain diatoms exhibit definite gliding movements, resembling the progressive movement of a tiny boat. The motion may proceed in one direction for a time, then in the opposite direction, or the direction may change at almost any angle. Only those diatoms that are in contact with some solid object move in this way. Those that live floating in the surface of the water do not exhibit such movements. No protoplasmic protrusion through the shell in the form of cilia or pseudopodia have been demonstrated to the satisfaction of the author.

Certain desmids like Closterium show slow movements by which they apparently creep up the walls of an aquarium. They also manifest orientation movements which are the result of a response to light. Cytoplasmic protrusions through the wall of desmids have not been demonstrated, so that neither the diatoms, desmids, nor blue-green algae have any protoplasmic organs of locomotion.

According to Lauterborn, the gelatinous substance exuded through the pore or pores in the diatom shell swells up greatly in the water, and, when resting against a support, the exuding mucilage pushes the cell forward and away from the support. Diatoms floating in the surface of the sea are said not to have pores in the shell for the exudation of the mucilage, and these diatoms do not exhibit the gliding or crawling motion.

Desmids that live as isolated cells may exhibit a gliding and pendulum-like movement, both of which may be influenced by light and gravity. Those like Closterium, for example, build up the mucilage at one end, which on swelling lifts the cell. These crescent-shaped cells may be seen standing on one end, the other end being free, when they may swing about and be inclined toward the light. In this position they may bend over, becoming attached at the other free end, and the process is repeated. By a continuous series of such somersaults the cells move over the surface.

CHAPTER XII

THALLOPHYTA—CHLOROPHYCEAE—GREEN ALGAE

The grass green algae include those which have a pure deep green or yellowish-green color. They vary in form, size, and structure from microscopic, unicellular species to larger massive cell masses resembling thickish cords or leaf-like bodies, as in the sea lettuce. The majority live in bodies of fresh water.

PROTOCOCCALES

The Protococcales include various forms, from unicellular, isolated individuals, such as Protococcus, to definitely organized colonies, as in Pediastrum and the water-net, Hydrodictyon. They occur chiefly in fresh water, ranging from a purely aquatic habitat to almost xerophytic conditions. Many that can live on moist surfaces are found on tree trunks, shaded earth, stones, etc. Certain forms constitute the algal constituent of many lichens, while others live in the intercellular spaces of aquatic seed plants, and still others impart the green color to such animals as fresh-water hydra and sponges.

Protococcus (**Pleurococcus**).—As one of the simplest representatives we shall select Protococcus, usually found in abundance on the shaded side of tree trunks, buildings, and walls, and on moist ground. The cells are globular when isolated, or flattened on one or more sides when adhering in clusters or in loosely and indefinitely organized colonies (Fig. 199, A to D). Protococcus is never motile in the vegetative condition. Each cell has a firm wall, a nucleus, and, according to West, a parietal and much lobed chloroplast. It is claimed also that two or more chloroplasts are present. Propagation is chiefly vegetative by the division of the cells* (Fig. 199, B, C, D). As stated, the plant is adapted to a wide range of conditions of moisture and temperature. On tree trunks, for example, the cells may remain viable in the xerophytic condition through long periods of drought in either winter or summer.

Scenedesmus.—This plant generally occurs in colonies of a small number of somewhat elongated cells adhering side by side (Fig. 199, F, G). The end cells of the colony in some species may bear two or more

* Protococcus taken from the bark of maple trees in July has been found by Professor J. M. Van Hook and the author to produce swarm spores.

short spines. Propagation is purely vegetative. In the simplest forms, each cell may divide lengthwise into two or more cells to form new colonies (Fig. 199, H).

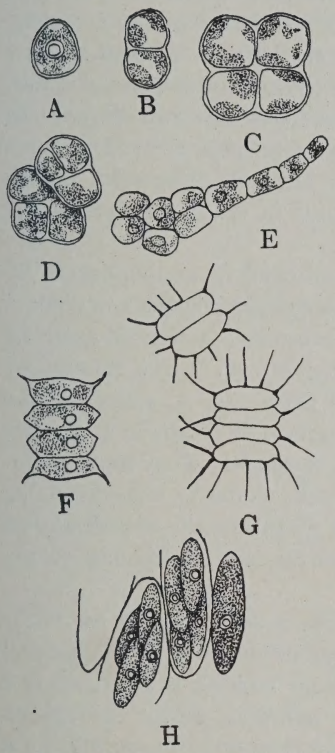


FIG. 199.—Protococcus and Scenedesmus. A–E, *Protococcus viridis* Ag. (*Pleurococcus vulgaris* Menegh.) A, a single cell; B–D, colonies of various sizes; E, the "protoderma" state. F, G, H, Scenedesmus; H, formation of new colonies from cells of an old colony. (A, C after Timberlake; B, D, E after Campbell; H, adapted from West.)

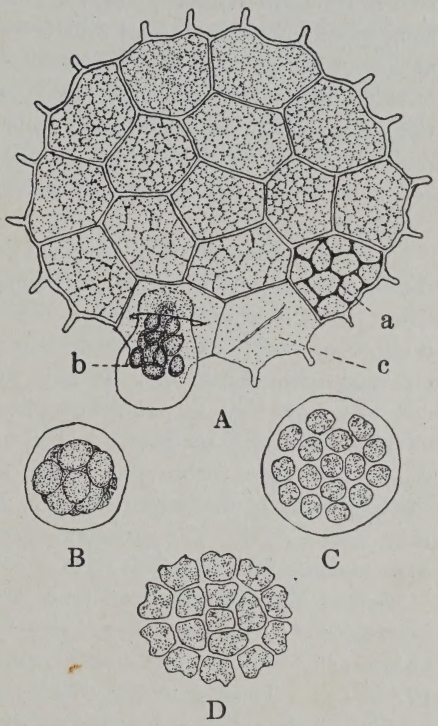


FIG. 200.—Asexual reproduction in Pediastrum. A, a 16-celled colony of *Pediastrum boryanum* (Turp.) Menegh., cells of which are forming new colonies; *a*, cell forming swarm cells; *b*, escape of swarm cells in gelatinous envelope; *c*, empty cell from which swarm cells have escaped. B, vesicle containing swarm cells after their escape from parent plant. C, swarm cells arranging themselves to form a new colony. D, a young colony after the dissolution of the gelatinous envelope.

Chlorococcum.—The spherical cells of Chlorococcum are found in water or in moist places. Some are said to constitute the algal portion of certain lichens. The plant propagates asexually by the production of one or more biciliate, motile cells, *swarm cells*, which escape from the parent cell, swim about for a time, and finally come to rest to form new individuals.

Chlorella vulgaris Beijr.—This is a widespread alga, which sometimes lives symbiotically in the cells of *Hydra viridis* and in such Infusoria as Paramecium and Stentor.

Pediastrum.—This plant consists of a definitely organized colony of cells in the form of a flat plate; the number of cells in the colony is usually some power of two. As an illustration we shall use a common species, as shown in Fig. 200, A. Here we see that the colony consists of a flat, circular disc of sixteen cells. Each peripheral cell has two spines. In the young colony each cell has but one nucleus; but later the cells become multinucleate. Individualized chloroplasts are not recognized in the cells, the chlorophyll apparently being diffused in the outer layer of the cytoplasm.

Asexual Reproduction.—Asexual reproduction is accomplished by motile cells, any cell of the colony being capable of producing a new colony. The process is as follows: nuclear division takes place in the cell until the number of nuclei equals the definite number of cells in the colony; by cleavage uninucleate cells are now formed (Fig. 200, A, *a* and *b*); the cell wall opens by a slit, and the biciliate swarm cells escape in a colorless envelope or vesicle, as shown in Fig. 200, A, *b* and B. They move about for a short time within the vesicle, and finally come to rest, arranging themselves as in the parent colony. In the meantime the cilia disappear (Fig. 200, C, D). The envelope then dissolves, and the young colony soon matures into the adult form.

Sexual Reproduction.—Sexual reproduction is accomplished by motile isogametes.* The gametes are developed as in the case of the asexual swarm cells, but they are smaller, and a larger number is produced in a parent cell. These gametes, which possess two cilia, escape through an opening in the cell wall into the water, where they unite in pairs to form zygotes. The steps leading to the formation of new colonies from the zygote are similar to those in Hydrodictyon, which are described in the following paragraphs.

Hydrodictyon.—The water-net is a definitely organized colony of many thousands of cylindrical cells united by their ends to form, as a rule, from three to six-angled meshes of a net (Fig. 201), the colony being in the form of a cylindrical or sleeve-like sac closed at both ends. These may attain a length of 20 or 30 centimeteres, the cells frequently measuring a centimeter in length. In almost all nets some irregularities occur, some of the meshes having more than six sides, and others being open, leaving cells with unattached ends. In each cell, which has a firm cell wall, the multinucleate cytoplasm is distributed in a thin layer along the wall, the remaining cavity of the cell being occupied by the large vacuole.

* Gametes equal in size.

In the cytoplasmic layer the chlorophyll is somewhat uniformly distributed, there being no individualized chloroplasts. Numerous pyrenoids are present in the chlorophyll-bearing layer.

Asexual Reproduction.—Any cell of the net may give rise to a new colony. By a process of cleavage the protoplasmic contents of the cell will divide into thousands (estimated at 7,000 to 20,000) of naked swarm cells, each having one nucleus and two cilia (Fig. 202, A, B, C). These motile cells move about actively in the cavity of the parent cell for a short time, after which they come to rest and begin to form a new net (Fig. 202, D, E). The cells lose their cilia, elongate, and become attached by their

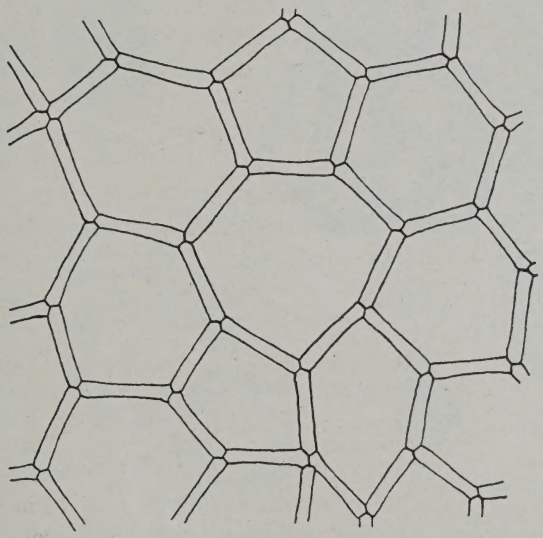


FIG. 201.—Portion of a colony of Hydrodictyon, showing the manner in which the cylindrical cells are attached to form a net.

ends in such a manner as to form the net (Fig. 203). The wall of the parent cell is now dissolved, and the young colony set free. The cells of the young net have but one nucleus each, but, with further growth and repeated nuclear divisions, the cells of the adult net become multinucleate.

Sexual Reproduction.—In the same manner as in asexual reproduction the protoplasmic contents of any cell may give rise to very many (30,000 to 100,000) biciliate swarm cells that are smaller than those formed in asexual reproduction. These are the gametes. They escape from the parent cell, move about freely in the water, and unite in pairs to form zygotes (Fig. 204, A, B, C). Gametes from the same cell or from different

cells may unite to form zygotes, and, because of this fact, Hydrodictyon is said to be monoecious.*

The zygotes move about for a time, then come to rest, and develop a firm cell wall (Fig. 204, C, D). According to Pringsheim, the zygotes will remain uninjured in the dry state if not exposed to the light. When

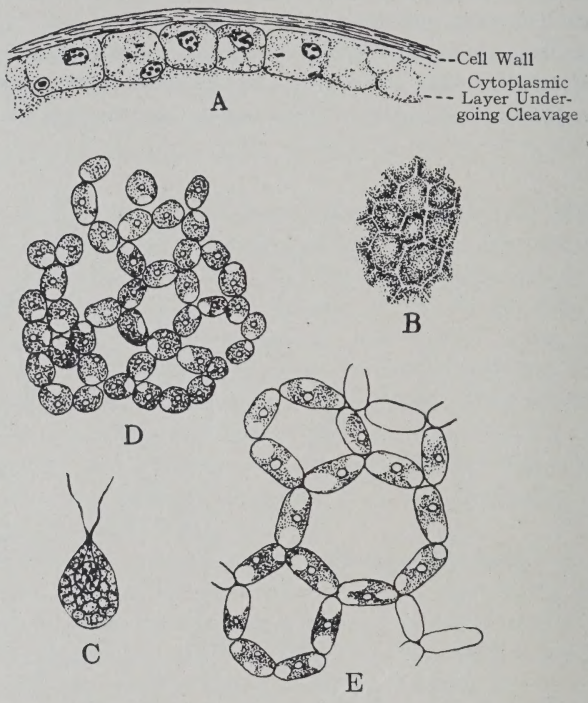


FIG. 202.—Asexual reproduction in *Hydrodictyon utriculatum* (L.) Lagerh. A, portion of wall layer of nucleated cytoplasm of a cell, showing cell cleavage; B, surface view of a few protoplasts that will become swarm cells. C, a mature swarm cell stained to show nucleus and starch grains. D, swarm cells coming together to form a net. E, a later stage than D, showing three meshes of a young net. (A and C after Timberlake; B, D, E, after Campbell. All greatly enlarged.)

they are kept in water, exposure to light does not impair their ability to germinate. Prior to germination the zygote undergoes a period of growth, by which it increases greatly in size and takes on a deep green color (Fig. 204, D). The contents then divide to form two to five biciliate swarm spores that escape through a rupture in the outer wall in a gelatinous

* A plant that produces gametes of both sexes is *monoecious;* it is a bisexual individual. When a plant produces gametes of but one sex, the individual is *dioecious*, two different individuals being necessary for the production of the functional gametes. Such individuals are unisexual.

vesicle (Fig. 204, E, F, G). This vesicle dissolves, and the swarm spores are set free. After swimming about for a time, each comes to rest and develops into a large cell having several conical or horn-like protuberances (Fig. 204, H). These cells have been named "polyhedra," because of their resemblance to a plant described under the name *Polyedrium*.

The contents of each polyhedron gives rise to swarm cells. The inner layer of the cell wall becomes mucilaginous, and by swelling, ruptures the outer cuticle-like layer and escapes as a gelatinous vesicle in which the swarm cells move about. They finally come to rest and form a new net, which is set free by the dissolution of the vesicle (Fig. 204, I). The nets arising from the polyhedra are relatively small (juvenile colonies), being composed of 200 to 300 cells, whereas the number of cells of a colony developed from a cell of an adult vegetative colony has been estimated by Alexander Brown to be as high as 30,000.

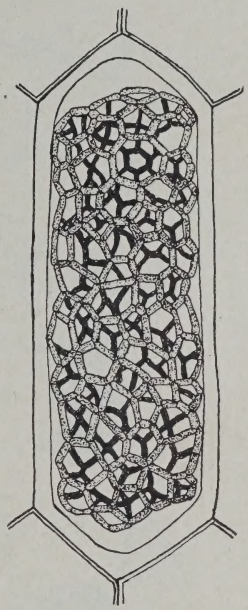


FIG. 203.—*Hydrodictyon utriculatum* (L.) Lagerh. A young net formed from swarm cells in a parent cell of an old net. (Adapted from Klebs.)

The life cycle of Hydrodictyon from adult colony to adult colony may be expressed as follows:

Hydrodictyon ⟨ gamete—escapes from cell / gamete—escapes from cell ⟩ zygote

→swarm spores→polyhedra→Hydrodictyon (juvenile colony)→swarm spores→Hydrodictyon (adult colony).

VOLVOCALES—ROLLING ALGAE

The Volvocales, like the Protococcales, occur in the form of unicellular individuals and colonies. They differ from the latter in being always motile in the active vegetative condition. The organization of the colony varies from that of simple, undifferentiated forms, as in Gonium, to those that are highly differentiated, as in Volvox.

Pandorina.—As an illustration of the complete life cycle in a simpler colony, Pandorina, which is commonly found among other fresh water algae, and easily recognized, may be selected. This plant consists of a globular colony of sixteen cells surrounded by a firm gelatinous envelope. Each cell is broadly ovoid or conical, or frequently angular by pressure of contact, with the narrow end next to the center. From near the center of the broad outer side of each cell spring two cilia which extend through the gelatinous envelope into the water. Near the base of the cilia is a

red pigment- or eye-spot. The chloroplast contains a pyrenoid. The colony is undifferentiated, the cells being alike in every respect (Fig. 205, A).

Asexual Reproduction.—In asexual reproduction each cell, by four successive divisions, gives rise to a new colony. Each cell of the new colony develops two cilia and the pigmented spot. A gelatinous envelope

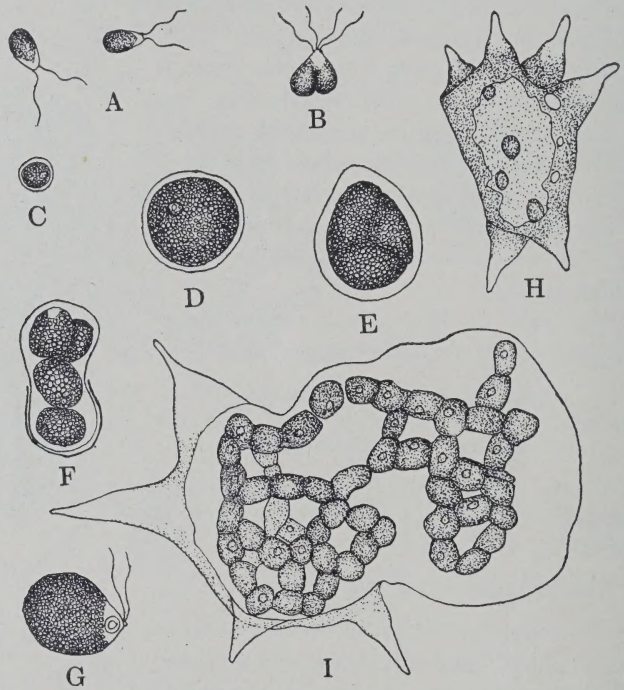


FIG. 204.—Sexual reproduction in *Hydrodictyon utriculatum* (L.) Lagerh. A, gametes; B, gametes uniting; C, zygote; D, zygote beginning to germinate; E, three of the four cells into which the contents of the zygote have divided; F, zygote in a later stage of germination; G, one swarm spore from a germinated zygote; H, mature polyhedron; I, formation of a small net from a polyhedron. (B, from Klebs; other figures from Pringsheim.)

is formed about each colony, and the new colonies are set free by the disintegration of the original gelatinous envelope (Fig. 205, B).

Sexual Reproduction.—Cells of the colony may also give rise to a large number of small, biciliate gametes, which escape from the envelope and move about freely in the water (Fig. 205, C). If the cells are of the same size they are termed *isogametes*, there being no distinction in sex. But, if, as may also happen, the gametes are of unequal size, the larger are

regarded as the female, and the smaller, as the male gametes. When the two gametes are unequal in size they are referred to as *heterogametes*.

The gametes unite in pairs to form zygotes, which continue to move about for a time but finally come to rest, developing a firm cell wall, and assuming a bright red color (Fig. 205, D, E, F, G). After a period of rest and the return of suitable conditions for growth, the zygotes will germinate,

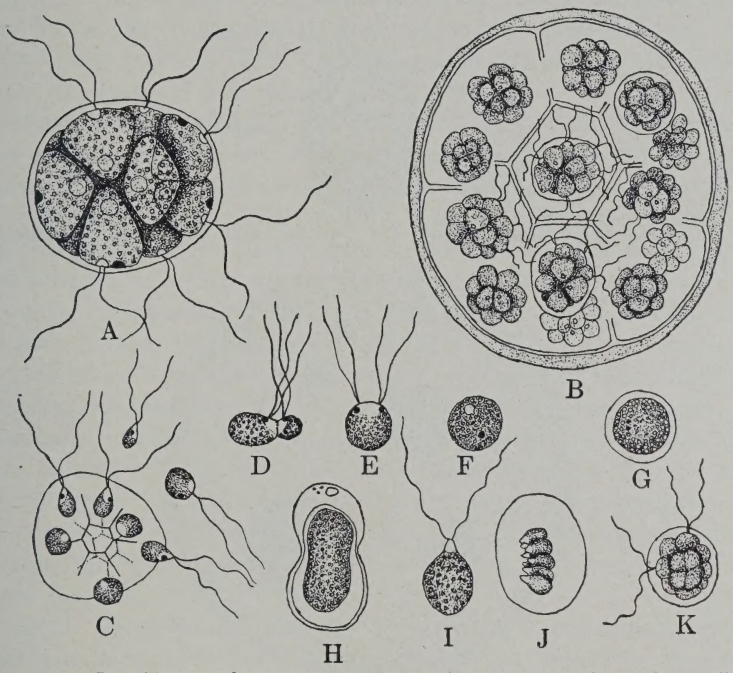


FIG. 205.—Life history of *Pandorina morum*. A, a mature colony of 16 cells; B, sixteen young colonies resulting from asexual reproduction, all held in the gelatinous envelope of the parent colony; C, gametes escaping from the gelatinous mass of the parent colony; D, E, F, union of gametes in pairs; F, young zygote; G, mature zygote, just prior to germination; H, germinating zygote; I, one of the swarm spores resulting from the germination of the zygote; J, K, young colonies produced by the division of single swarm spores. All figures ×850. (After Pringsheim.)

giving rise to two or four swarm spores (Fig. 205, G, H, I). Each swarm spore may now divide, giving rise to a new colony of sixteen cells (Fig. 205, J, K). It is reasonable to suppose that the zygote represents the diploid structure of Pandorina.

A diagram of the life cycle of Pandorina may be written as follows:

Pandorina ⟨ gamete / gamete ⟩ zygote → 4 swarm spores → 4 Pandorina.

Chlamydomonas.—Chlamydomonas is a rather common unicellular form. The cell bears two cilia and has a large, cup-shaped chloroplast

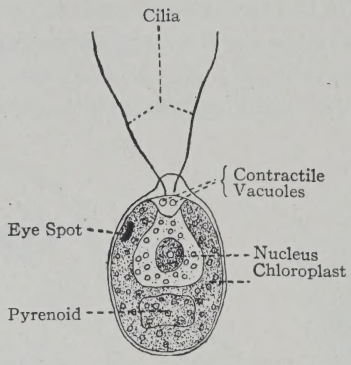


FIG. 206.—*Chlamydomonas angulosa* Dill. (After Dill according to Oltmanns.)

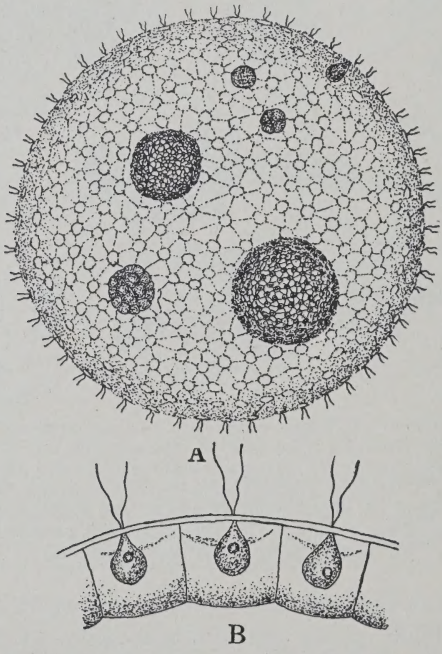


FIG. 207.—Volvox. Structure and asexual reproduction. A, adult colony containing two young colonies, and four stages in the development of the colony from vegetative cells. B, portion of the gelatinous periphery of the colony, showing position of the vegetative cells.

in the thick bottom of which is a pyrenoid. Near the anterior end of the cell are contractile vacuoles and a red pigment spot (Fig. 206). Chlamydomonas reproduces both sexually and asexually after the manner of

Pandorina. *Chlamydomonas nivalis* (Bauer) Wille (Haematococcus) is usually blood red in color, owing to a pigment, *haematochrome*. The thick-walled, non-motile forms may occur in large quantities on snow in high altitudes, when they are known as "red snow."

Haematococcus pluvialis Flotow (*Sphaerella lacustris* Hazen), also deep red in color, is commonly found in shallow pools, where the resting cells form a dull red coating on the bottom or on any contained objects when the pool dries up. This fact has given rise to the expression "red rain." Haematococcus differs from Chlamydomonas in having protoplasmic threads that pass out into the cell wall.

Volvox.—The most highy differentiated forms of the Volvocales are found in the genus Volvox. *Volvox globator*, the species most commonly encountered, consists of thousands of very small, pale green, pear-shaped cells embedded near the surface in a hollow sphere of gelatinous substance. Each cell has a chloroplast, a nucleus, an eye-spot, and two cilia attached at its anterior end (Fig. 207, A, B). The cells are connected with one another by cytoplasmic threads. The colonies are often more than half a millimeter in diameter, and may readily be seen with a hand lens as pale green spheres rolling through the water. Because of the cytoplasmic connections between the cells, and the highly differentiated gametes, it is questionable whether Volvox should be regarded as a colony (coenobium) or as a definite multicellular individual. Volvox is not in the form of an exact sphere, but one which is very slightly oval. The smaller end contains few or no vegetative reproductive cells. This smaller end of the oval may be regarded as the anterior end of the plant and the opposite side the posterior end.

Asexual Reproduction.—Certain vegetative cells will increase greatly in size and move into the hollow of the sphere. Here, by successive divisions, a small, rounded, flat disc is formed, then a bowl, and finally a closed sphere. Three or more colonies may thus be developed within the central cavity of one parent colony (Fig. 207, A). The parent colony, rolling gently through the water, with two or three smaller colonies rolling within it, is a fascinating sight when seen with the microscope.

Sexual Reproduction.—Volvox develops two kinds of gametes: small motile sperms and large, non-motile eggs. The sperm is a pale yellowish, club-shaped cell with a slender, tapering anterior end. It has two cilia inserted laterally, and an eye spot (Fig. 208, B). A large number of sperms are formed from a single vegetative cell which enlarges and passes into the interior of the colony, where it undergoes repeated divisions in one direction (Fig. 208, A). Certain other vegetative cells, which have enlarged and passed into the central cavity, become eggs (Fig. 208, A). There they unite with sperms to form zygotes. The zygotes assume a

reddish color and develop a thick wall, the outer layer of which becomes spiny (Fig. 208, C). After a period of dormancy the zygote germinates, giving rise to a new colony.

Response to Light.—Motile plant cells, especially among the algae, whether respresenting the vegetative or reproductive condition, are usually influenced in the direction of their movements by chemical substances and by forces of the environment which affect them as stimuli. The cells are said to *respond* to the given stimulus. For example, if Pandorina, or any other of the Volvocales, be held in a glass vessel so that

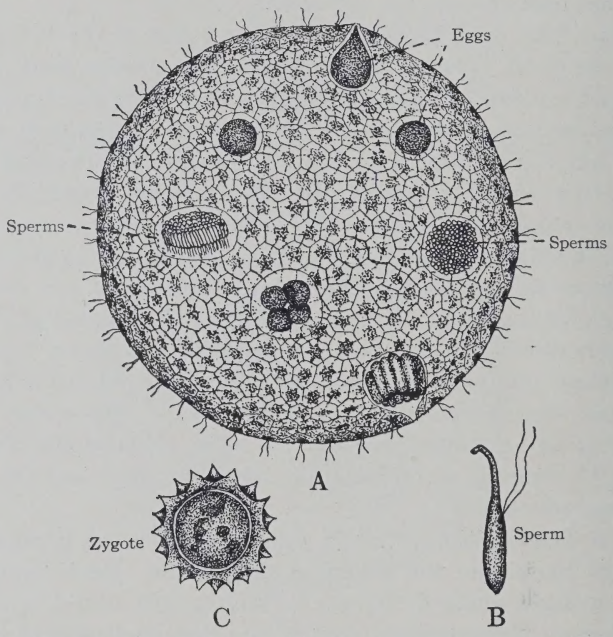


FIG. 208.—Sexual reproduction in Volvox. A, monoecious colony bearing eggs and sperms; B, one sperm, showing shape, eye-spot, and cilia. C, mature zygote provided with a thick spiny wall. (Redrawn from chart by Leuchart.)

the light enters from one side, as near a window or an artificial light, the plants will soon collect along the wall of the vessel next to the window or next to the source of light. If observed in a hanging drop under the microscope, they will be seen to move toward the edge of the drop next to the source of illumination. The light does not cause the plants to move, it merely influences the *direction* of their locomotion. If the light be too dim, there will be little or no response, and if it be too intense, the plants may move in the opposite direction, that is, away from the source of illumination. The response that motile plants make to light in this manner is termed *phototaxis*. Movements toward the source of illumina-

tion, or toward any source of stimulus, represent a *positive* response (as positive phototaxis); movement directed away from the source of the stimulus is a *negative* response (as negative phototaxis).

It should be remembered that an organism will respond normally to stimuli only when the intensity of the energy falls within a certain range. The extremes represent intensities beyond which no response is perceptible. The lower limit is the *minimum*, the upper, the *maximum*, and that intensity or degree of energy which calls forth the best response is the *optimum*. Strong electric light concentrated upon the plants may kill them instantly.

Generally speaking, motile plant cells provided with eye-spots are more sensitive to light than those in which such a body is absent. This fact has led to the view that the eye-spot represents a part of the cytoplasm which is especially sensitive to light. Do you think the response to light is of any advantage to the plants in question in their adaptation to the environment? Or has the response to light any "survival value"?

CONFERVALES—CONFERVOID ALGAE

The confervoid algae include the majority of the common filamentous forms, which are very widely distributed in both fresh and salt water. They represent a wide range of variability both in vegetative structure and in methods of reproduction. In vegetative structure they range from very simple unbranched filaments to a more massive and leaf-like thallus, as is illustrated in Ulva (sea lettuce). As concrete cases for detailed presentation we shall select Cladophora and Oedogonium, the former representing a simple method of sexual reproduction in which both gametes and gametangia are undifferentiated, while in the latter the sexual cells are highly specialized. Other forms commonly found in ponds and streams will be described very briefly.

Cladophora.—Cladophora consists of branched filaments differentiated into base and apex. The filaments are usually attached to some object in the water by means of the basal cells, which are modified into organs of attachment, or holdfasts. Some forms branch very profusely and form relatively short, dense, bushy tufts (Fig. 209, A). During the spring and early summer months the growth of some forms is so prolific that the immense, ropy masses almost clog the small streams in which the plant is common.

The branches arise normally from the upper (distal) ends of the cells (Fig. 209, B). Growth in length of the filaments is confined chiefly to the terminal portions, though cell divisions not infrequently occur in the older parts of the plant. For details of cell division see Chapter II, page 24.

Structure of the Cell.—The cells have a firm and rather thick, stratified wall, to which may often be attached diatoms and other small algae, together with particles of foreign matter, all of which help to impart a noticeable harshness to the mass. Numerous nuclei, pyrenoids, and chloroplasts are present in each of the larger adult cells. The chloroplasts are rounded, but in older, well nourished cells they may become

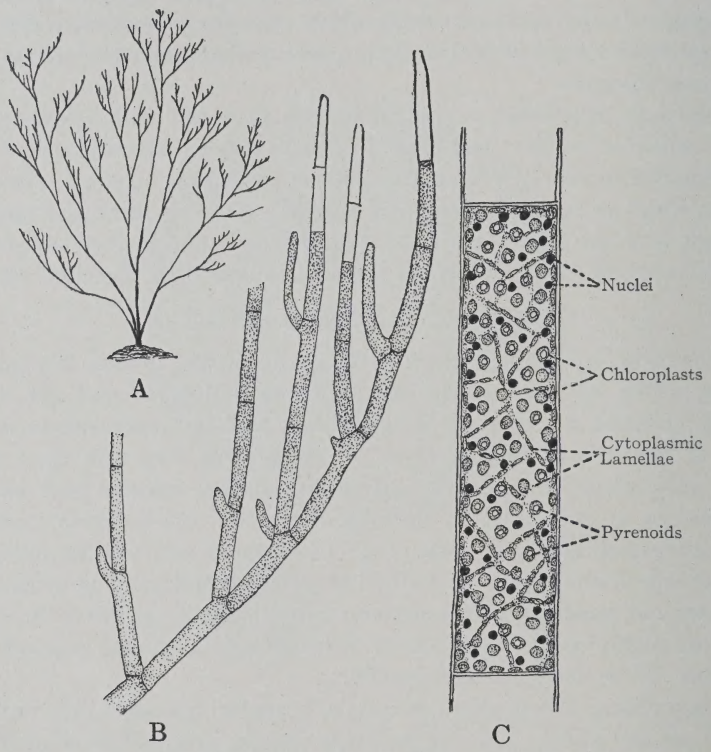


FIG. 209.—Cladophora (Sp.) A, sketch of a tuft of plants attached to a rock or other substratum. B, small portion of a plant, enlarged, showing method of branching; swarm spores or gametes have escaped from the empty cells at or near the tips of some of the branches. C, an actively growing vegetative cell, enlarged, showing the numerous nuclei, chloroplasts, and cytoplasmic lamellae; the chloroplasts distributed along the latter are seen from their edges.

polygonal because of crowding. The central part of the cell is occupied by a large vacuole, which, however, is traversed by flat cytoplasmic plates, or lamellae, which meet and intersect in such a manner as to divide the vacuole into cell-like compartments. The chloroplasts are confined principally to the wall-layer of cytoplasm, although a few may be located upon the lamellae (Fig. 209, C).

Asexual Reproduction.—Cladophora reproduces asexually by means of swarm spores. These are commonly developed in the cells of the younger branches. In the formation of swarm spores the contents of the cell, by cleavage, give rise to a number of naked cells, which escape through a small opening near the upper end. The cell that produces spores is called

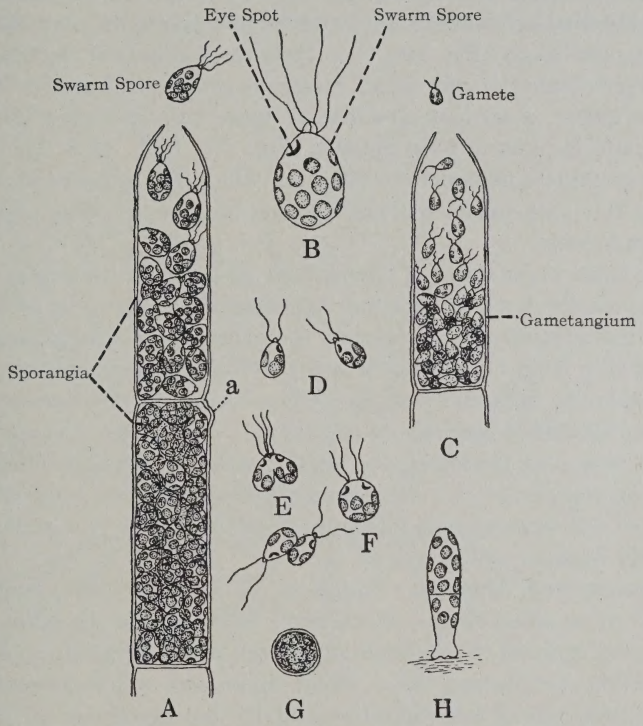


FIG. 210.—Cladophora. Asexual and sexual reproduction. A, two cells at the end of a branch, which have become sporangia. Swarm spores escaping from the terminal cell; those in the cell below almost mature; *a*, place at which the opening of the sporangium will be formed. B, a single swarm spore, greatly enlarged, showing the four cilia, the eye-spot, and the chloroplasts. C, a gametangium, from which gametes are escaping. D, gametes greatly enlarged, showing the two cilia, the eye-spot, and the chloroplasts. E, gametes uniting in pairs. F, a young zygote in which the characteristics of the gametes are still seen. G, mature zygote. H, a young plant resulting from the germination of a swarm spore or from a zygote would be similar to this in appearance. (Figures somewhat diagrammatic; from a species collected in the Bay of Naples.)

a sporangium (Fig. 210, A). The swarm spores nave four cilia, which arise near the base of a small beak at the anterior end, an eye-spot, one nucleus, and two or more chloroplasts (Fig. 210, B). In some species asexual swarm spores with but two cilia have been reported. After moving about for a time the spore comes to rest and develops into a new

filament. On coming to rest the swarm spore usually attaches itself to some object, the beak at the anterior end developing into the holdfast.

Sexual Reproduction.—Sexual reproduction is accomplished by motile isogametes, each provided with two cilia. They are much smaller than the asexual swarm spores. As in the case of asexual reproduction, the cells of the smaller branches may, without undergoing any external change, become gametangia (Fig. 210, C). Here the contents of the cell give rise to a larger number of cells which escape as gametes. Each has two cilia, a red eye-spot, a nucleus, and one or more chloroplasts (Fig. 210, D). They unite in pairs to form zygotes (Fig. 210, E, F, G). The zygote is said to germinate immediately (Fig. 210, H). The gametes may start to develop into new plants without uniting, but the resulting plantlets are small and feeble.

The fresh water forms of Cladophora do not produce swarm spores or gametes readily, but in certain marine species, if the plants be brought from the sea and placed in shallow dishes, the swarm spores and gametes will be developed in large numbers over night. Both swarm spores and gametes are sensitive to light and lend themselves readily to experimentation.

Some species of Cladophora are annual, while others seem to live from year to year. In the latter, the larger portion of the plant dies, but the basal portions persist, the cells becoming filled with food material. These cells give rise later to new filaments vegetatively; or it is probable that they will develop swarm spores.

Aplanospores, Akinetes.—Many of the Confervoideae develop what are known as *aplanospores*, which serve to propagate the plant. In the production of these the contents of the cell contract and form a new cell wall within the parent cell. These aplanospores lie dormant during periods unfavorable for vegetative activity but germinate on the return of favorable conditions, growing into new plants. If vegetative cells merely thicken the wall of the old cell without forming a new wall as described for aplanospores, and give rise to new plants in like manner, such cells are called *akinetes*.

Ulothrix.—Ulothrix consists of delicate, unbranched filaments, whose rather short, uninucleate cells are all alike except the basal or holdfast cell. The chloroplast is band-shaped with one or more pyrenoids. It frequently occurs in aquaria and in tanks or troughs used for watering stock. Large species are often used in class room studies to demonstrate the formation of spores and gametes.

Conferva.—Members of this genus consist also of unbranched filaments, in which the uninucleate cells have two to several disk-shaped chloroplasts, but no pyrenoids. Reserve food, if present, is in the form

of oil rather than starch. The plant is found in ponds and streams along with other algae.

Chaetophora.—The copiously branched filaments of this alga are embedded in a rather firm gelatinous mass. The plant may be recognized as green, rounded masses of jelly, varying in size from two to ten millimeters in diameter, attached to stems and leaves or other objects in clear, running water in the spring. The branches of the filaments end in long,

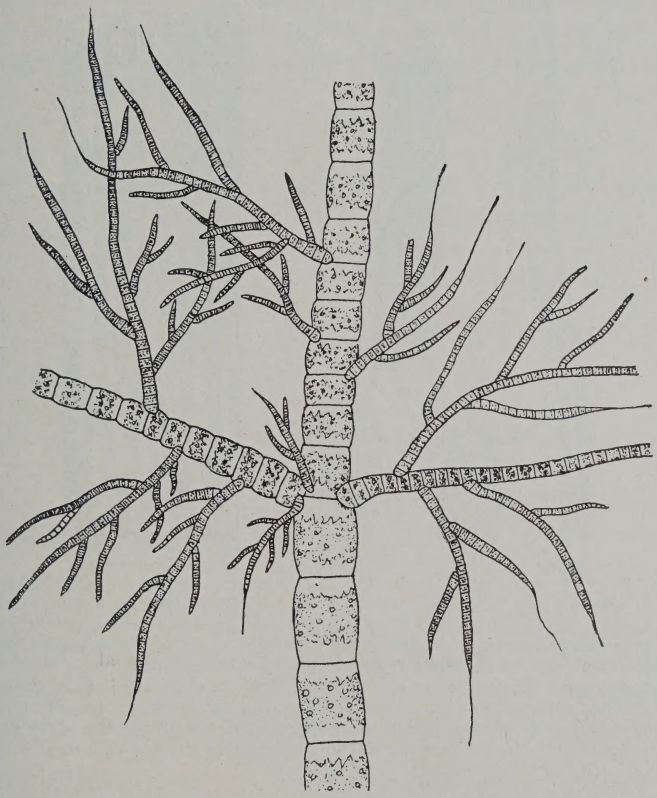


FIG. 211.—Draparnaldia. Portion of a plant showing structural habit.

slender, colorless cells. The single chloroplast in the cell consists of a parietal band with one or more pyrenoids.

Stigeoclonium.—Stigeoclonium consists of branched filaments, but with little distinction between the branches and main filaments. The filaments are surrounded by a gelatinous substance, but not united into a compact mass as in Chaetophora. They end in slender, colorless cells.

Draparnaldia.—Draparnaldia is generally abundant in running water in early spring. It consists of a definite main filament or axis with tufted

side branches of more limited growth. The main axis bears secondary axes which repeat the characteristic structure of the main axis. The whole plant is coated over with the gelatinous substance, and the branches may end in slender, colorless cells. In the cells of the main axis the chloroplast is in the form of a cylindric or parietal band, which may be perforated. Pyrenoids are present (Fig. 211).

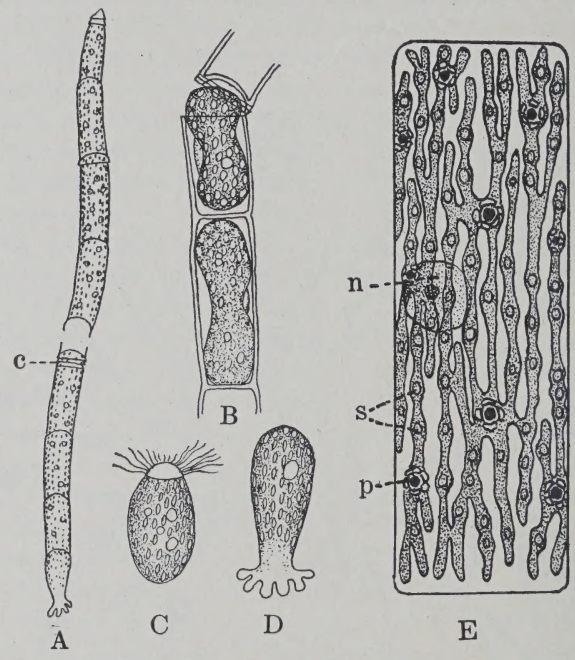


FIG. 212.—Oedogonium. A, the upper and lower ends of a vegetative filament; *c*, the cap-like markings at the upper end of certain cells. B, two cells, illustrating the formation of swarm spores, one spore being formed in each cell. C, a swarm spore, showing anterior colorless spot and the circle of cilia at its base. D, germination of a swarm spore. The colorless anterior end is sensitive to contact and develops into the holdfast. E, outline of cell, showing net-like chloroplast; *n*, nucleus; *s*, stroma starch; *p*, pyrenoid. (After Oltmanns.)

Ulva.—The sea lettuce has the form of a large, leaf-like cell surface, two layers of cells in thickness. All species are marine.

Enteromorpha.—The plants of this genus are ribbon-shaped, either cylindrical or flattened. When young the plant body is two cells in thickness, but later it becomes hollow, the wall consisting of one layer of cells.

Oedogonium.—Oedogonium consists usually of deep green, unbranched filaments, strictly differentiated into base and apex, and ordinarily attached to some submerged object such as the stems and leaves of other plants. Adult plants may sometimes break away and float in masses.

The basal cell of the filament, frequently in the shape of an Indian club, serves as the holdfast. The terminal cell may be rounded, pointed or elongated into a slender hair-like structure. The basal cell never undergoes division. The end of the basal cell which is attached is either flattened into a disk or developed into a number of short, finger-like branches (Fig. 212, A).

The cell wall consists of a relatively thick cellulose layer with a thin cuticle on the outside. Across the upper ends of certain cells may be seen two to several fine parallel lines by which Oedogonium may readily be distinguished from other unbranched filamentous algae similar to it in

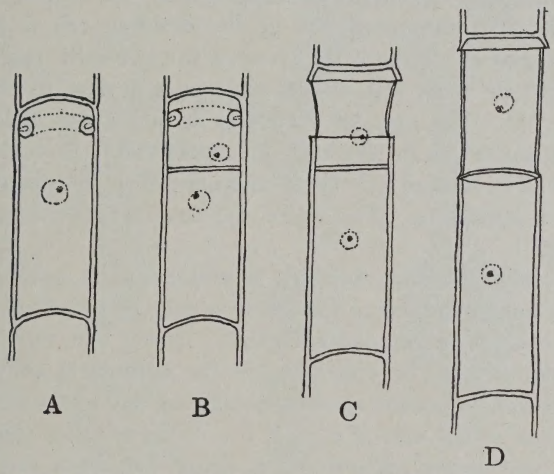


FIG. 213.—Cell division in Oedogonium. A, cell with thick ring of cell wall substance formed inside at the upper end. B, small cell and large cell formed by division of A. C, a circular split has occurred in the old cell wall entirely around the cell just opposite the middle of the ring; the ring has stretched in length to make a new wall for the upper cell. The part of the old wall above the circular split now forms a cap. D, the upper cell has elongated, and its lower end has moved upward to the top of the old cell wall. There have thus been formed two cells, the upper with an entirely new lateral wall and the lower completely enclosed in the old wall of the parent cell.

appearance (Fig. 211, A, *c*). These lines represent the edges of the so-called "caps."

The cytoplasm is chiefly disposed as a thin parietal layer in which the chloroplast is imbedded. The chloroplast is variable, but always parietal, and usually in the form of a net or reticulum (Fig. 212, E). In the larger species the pieces of the reticulum may become separate and distinct. One or more pyrenoids may be present. The nucleus of the cell is usually centrally placed.

Cell Division.—Any cell of the filament, except the basal cell and in some species the tip cell, is capable of division; but only certain cells

undergo several successive divisions. These are the ones with the transverse lines or "caps" to which reference was made above. The caps indicate the number of times the cell has divided (Fig. 211, A, *c*). When a cell divides, one of the resulting cells possesses the old cell wall; the other has an entirely new cell wall except for the cap at the upper end. The new wall is formed during division as follows: in the upper end of the dividing cell a thick solid cellulose ring is formed next to the lateral wall (Fig. 213, A); after the nucleus has divided, or as it divides, a circular cut or split occurs in the cell wall along the line of contact between the wall and the cellulose ring (Fig. 213, B); the ring now stretches into a cylinder, which, with the cap at the top, becomes the wall of the upper of the two cells; the transverse wall of the dividing cell is formed just below the circular cut, so that the lower of the two cells has the old wall of the parent cell, while the wall of the upper is new, as stated above (Fig. 213, C, D). The new cell elongates in such a way that the transverse wall is moved up in line with the upper end of the old wall. The transverse wall is formed by the fibers connecting the daughter nuclei, and not as in Spirogyra. The tip of the terminal cell of the filament is usually a cap.

Asexual Reproduction.—Asexual reproduction is accomplished by large swarm spores, one being formed in a cell. Any cell of a filament, except a tip cell, may form a swarm spore. During the transformation of the cell contents into the swarm spore the cytoplasm contracts away from the cell wall by means of self-plasmolysis, and a lens-shaped, colorless area is seen at one side (Fig. 212, B). This colorless spot represents the anterior end of the mature swarm spore, and from the base of this spot a circle of many cilia will arise. The cell wall splits transversely near the upper end and the swarm spore escapes. It is generally oval in shape, with the colorless beak at the anterior end; from the base of the beak spring the cilia (Fig. 212, C).

The swarm spore does not have an eye-spot. After a short period of movement the spore comes to rest and germinates. The anterior colorless end becomes the holdfast of the new plant (Fig. 212, D). It will be seen that the longitudinal axis of the spore and of the new plant represents the transverse axis of the parent cell.

Sexual Reproduction.—The type of sexual reproduction seen in Oedogonium is one of the highest found in any of the green algae, both the gametes and the gametangia being differentiated sexually. The gametangium bearing the egg, or female gamete, is the *oögonium;* that producing the sperms, or male gametes, is the *antheridium.*

Both monoecious and dioecious species are found in the genus. A dioecious species is selected for presentation here.

In this the female plants are of the normal size of the adult filament, but the functional male plant, known as the "dwarf male plant," is very small, consisting of only two or three cells. The dwarf male plants are usually, though not always, attached to the female plants just below the oögonium (Fig. 214, A). The oögonium is rounded or barrel-shaped, and larger than the ordinary vegetative cells. It is usually formed from a cell that has divided two or more times, as shown by the cap-like markings at the upper end (Fig. 214, A). The contents round off, and the

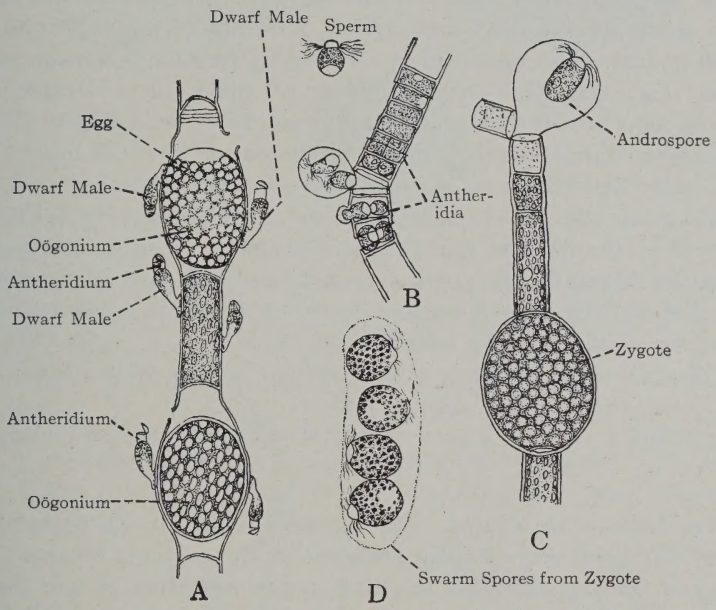


FIG. 214.—Oedogonium. Sex organs and germination of zygote. A, portion of filament with two oögonia, and attached dwarf males, bearing antheridia. B, portion of a filament that has given rise to antheridia, each containing two sperms. C, portion of a filament showing a mature zygote in an old oögonium, and an androspore developing from another cell. D, four swarm spores resulting from the germination of a zygote. (B, C, D, after Pringsheim.)

chloroplast withdraws slightly from the upper end, forming the colorless "receptive spot." An opening in the cell wall is formed at one side near the upper end of the oögonium, and the egg is ready for fecundation.

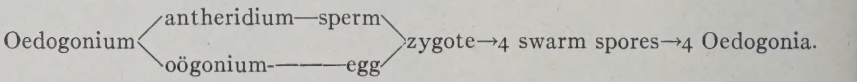
The "dwarf male" in this species ordinarily consists of a basal cell and an antheridium. The antheridium bears two sperms (Fig. 214, A). The sperm is a very small, colorless, oval cell, with a circle of cilia at its anterior end. When the antheridium opens, the sperms escape, and one of them enters the oögonium and penetrates the egg, its cytoplasm mingling with that of the egg, and its nucleus fusing with the egg nucleus.

When fecundation is completed, the zygote develops a firm cell wall and passes into a period of dormancy. The mature zygote is reddish-brown in color, and various external markings are developed in some species. The reserve food is a fatty oil dissolved in a reddish-brown pigment (Fig. 214, C).

Formation of the Dwarf Male.—The dwarf male plants which produce the sperms are developed from swarm spores formed by a plant similar to the oögonial plant. Certain cells divide transversely into a small number of short cells (androsporangia) each of which produces a small swarm spore, known as an *androspore.* Androspores are similar to the asexual swarm spores described in a preceding paragraph, though much smaller (Fig. 214, C). They escape, move about in the water, and finally become attached and develop into the dwarf male plants. When androspores become attached to the oögonium, or to a cell near it the dwarf males are likely to be found as shown in Fig. 214, A.

Monoecious Species.—In monoecious species of Oedogonium antheridia are borne by the filament that produces oögonia. In such cases certain cells of the filament undergo transverse divisions into several short cells. Each of these is an antheridium and bears two sperms (Fig. 214, B). The sperms are smaller than the androspores.

A diagram of the life cycle of Oedogonium may be written thus:



Germination of the Zygote.—The zygote is set free by the decay of the wall of the oögonium. During germination the contents become green again and undergo divisions resulting in the formation of four swarm spores, which escape in a delicate vesicle when the cell wall is ruptured (Fig. 214, D). The vesicle dissolves, and the four swarm spores move about for a short time, finally coming to rest and developing into new plants. The zygote is doubtless the diploid structure, while the whole plant is the haploid structure.

Coleochaete.—Coleochaete is of special interest because its life history is suggestive of one way by which plants like the liverworts may have been developed from an alga-like ancestor.

The plant occurs in fresh water, commonly attached to the leaves and stems of aquatic plants. It consists of a flat, rounded or lobed disc of cells arranged in radial rows, or of radiating, branched filaments attached in part side by side (Fig. 215, A, C). In some species certain cells bear long, slender spines. The uninucleate cells contain each a parietal chloroplast with one or two pyrenoids.

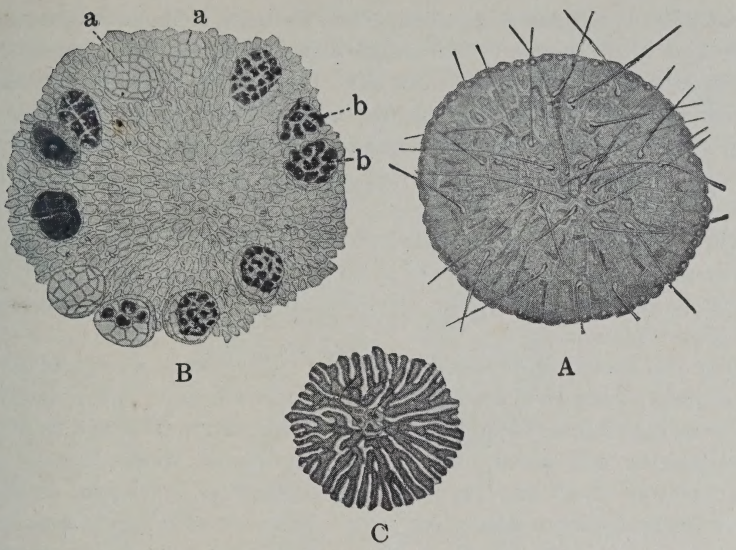


FIG. 215.—A, *Coleochaete scutata* Breb. B, *Coleochaete soluta* (Breb.) Pringsheim, showing zygotes in different stages of germination; *a*, *a*, zygotes from which swarm spores have escaped; *b*, *b*, zygotes containing nearly mature swarm spores. C, young plant of *C. soluta*. (From Pringsheim.)

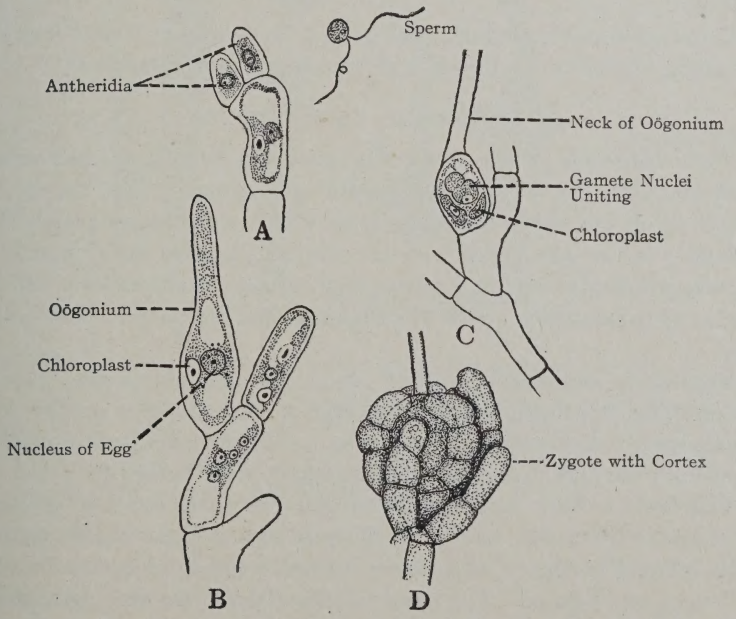


FIG. 216.—Fecundation in *Coleochaete pulvinata* A. Br. A, cell bearing two antheridia. B, portion of branch bearing oögonium. C, oögonium in which egg and sperm nuclei are fusing. D, oögonium with cortical cells growing up about it. (A, B, C, adapted from Oltmanns; D, from Pringsheim.)

Asexual reproduction is accomplished by large biciliate swarm spores.

Sexual Reproduction.—The antheridia are short, flask-shaped cells, and each bears a sperm having two cilia (Fig. 216, A). The oögonium is a flask-shaped cell with a long, slender neck that opens at the distal end (Fig. 216, B and C). After fecundation the basal part of the oögonium becomes surrounded by a cortex of cells developed near its base (Fig. 216, D).

On germination, after a period of dormancy lasting over winter, the zygote gives rise to a structure of 16 to 32 cells, each of which produces a swarm spore (Fig. 215, B, *b*). On being set free, the swarm spores give rise to new plants.

The cell structure developed from the zygote bears a resemblance to the diploid structure of a simple liverwort like Riccia. In the liverwort, however, the diploid structure has a wall of vegetative cells, and from each spore-bearing cell within, a tetrad of non-motile spores is produced. The covering about the zygote in Coleochaete is developed, as stated above, from adjacent vegetative cells. The reduction in the number of chromosomes from the double to the single number in Coleochaete occurs in the first nuclear division in the germinating zygote, so that the swarm spores resulting from the zygote constitute the beginning of the haploid structure.

Coleochaete soluta, as shown in Fig. 215, B, suggests a simple liverwort, containing diploid structures in different stages of development.

SIPHONALES—GREEN FELTS

The Siphonales include a large number of green algae which present a wide diversity in size, form, and general appearance. They are common in both fresh and salt water, the larger and more complex plants living preferably in the warm seas. In structure all are generally similar in one respect; namely, the plant consists of a tubular, multinucleate cell or a number of tubular cells woven or grown together in a more or less compact mass.

Vegetative propagation occurs in a number of species. Asexual reproduction is accomplished by swarm spores. In the smaller forms sexual reproduction is brought about by motile isogametes; in the highest forms both sex organs and gametes are highly differentiated.

Vaucheria.—As a concrete illustration we shall select a species of Vaucheria, such as *V. sessilis* or *V. geminata.* These plants grow on moist, shaded earth, or attached to stones or other objects over which cool, clear water flows. The latter species often forms floating masses.

As shown in Fig. 217, A, the plant is a tubular, branched filament, containing many small, rounded chloroplasts and numerous small nuclei,

which are visible only when stained. Oil drops are present among the chloroplasts. The normally developed filaments are without cross walls except where reproductive structures are formed, or where the filament has suffered some injury. The filament may, therefore, be regarded as a multinucleate cell (coenocyte). The species that grow on moist earth

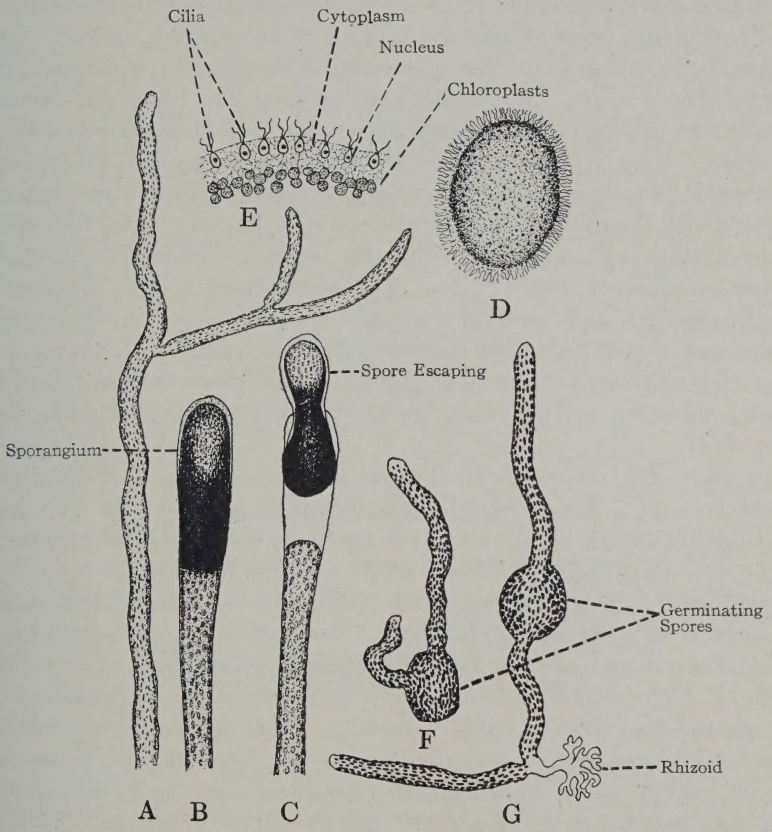


FIG. 217.—Vaucheria. Vegetative structure and asexual reproduction. A, portion of a filament of *Vaucheria sessilis*, showing mode of branching; B, C, D, *Vaucheria ungeri* Nob.; B, end of filament forming sporangium; C, swarm spore escaping from sporangium; D, swarm spore killed with iodine, showing cilia; E, F, G, Vaucheria sessilis; E, peripheral portion of swarm spore stained to show relation of cilia to nuclei; F, germinating swarm spore; G, young plant developed from swarm spore. (B, C, D, from Thuret; E, Strasburger, Macmillan Co.; F, G, from Sachs.)

are attached to the soil by means of branched *rhizoids* (Fig. 217, G). A rhizoid serves as an organ for the absorption of water from the soil as well as for a holdfast.

Asexual Reproduction.—Species that grow on moist soil, such as *Vaucheria repens* Hassall, or *V. sessilis* (Vaucher) De Candolle, may

develop swarm spores readily under experimental conditions. A thin layer of soil covered with a turf of the filaments is kept in the light in a moist chamber for a few days until numerous ends of filaments have assumed an upright position. The plants still attached to the soil, are then completely submerged in water and placed in the dark. In 12 to 24 hours, swarm spores will be formed. In the formation of the sporangium, the end of the filament becomes somewhat club-shaped, and of a dark green color, owing to the accumulation of chloroplasts and denser cytoplasm (Fig. 217, B). Many nuclei also migrate into the end of the filament. A cross wall is next formed, separating the end from the rest of the filament. This cell, which is now the sporangium, opens at the tip, and the entire contents escape as a globular or oval swarm spore with numerous pairs of cilia distributed over its entire surface (Fig. 217, B, C, D). Each pair of cilia corresponds to a nucleus, which is situated beneath the plasma membrane (Fig. 217, E). The swarm spore is, therefore, multinucleate. It is dark green in color, and after escaping from the sporangium moves slowly through the water for a short time. On coming to rest it germinates at once, sending out one or more slender tubes. If grown upon earth, the young plant may soon develop rhizoids (Fig. 217, F, G).

Sexual Reproduction.—To illustrate sexual reproduction, *Vaucheria sessilis* or *V. geminata* var. *racemosa* may be selected. In *V. sessilis* the oögonia and antheridia may be formed near each other on the filament (Fig. 218, A). The antheridium, which is hooked or curved, is borne on a short pedicel. The numerous sperms produced in each antheridium escape through an opening in the distal end. The sperms are very small, somewhat pear-shaped, and provided with two laterally attached cilia (Fig. 218, C). The oögonium is sessile and obliquely oval. A rounded beak at the top indicates the place of opening. The oögonium bears a single large, uninucleate egg. The primordium of the oögonium is multinucleate, but all except one of the nuclei either pass back into the filament before the wall separating the oögonium from the filament is formed, or they disintegrate. At the upper end of the egg, near the opening, is a colorless spot, the receptive spot.

After fecundation, the zygote develops a thick cell wall, becomes dark brown in color, and passes into a dormant condition. On germination the zygote becomes green and grows directly into a new plant (Fig. 218, D).

In *Vaucheria geminata* var. *racemosa*, the antheridium and oögonia are borne upon a short side branch arising at right angles to the main filament (Fig. 219, A, B). This side branch ends in a more slender part making a ram's horn turn (Fig. 219, A). The terminal portion of the turn is cut off by a transverse wall to become the antheridium. As in *V.*

sessilis, the antheridium is colorless and bears a number of sperms that escape through a terminal opening. Close below the base of the antheridium a number of oögonia are developed in a circle. Each is generally obliquely oval and is mounted on a short stalk (Fig. 219, B). It contains a single egg which is believed to have only one nucleus.

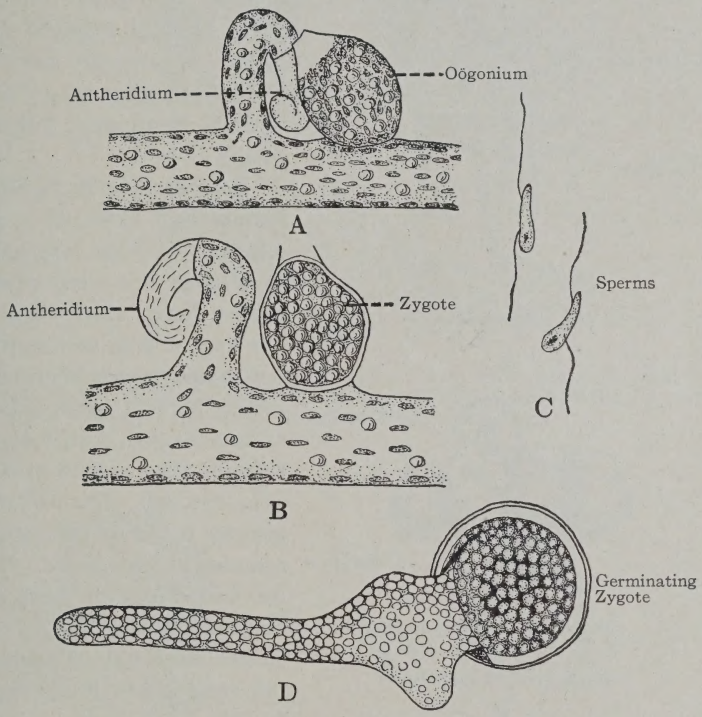


FIG. 218.—Sexual reproduction in Vaucheria. A, B, D. *Vaucheria sessilis* (Vauch.) D. C. A, portion of a filament bearing an antheridium and an oögonium; B, later stage than A with empty antheridium and an oögonium containing zygote; C, two sperms. D, germinating zygote. (Figures adapted: A, B, from Campbell's "University Text-book of Botany." By permission of the Macmillan Company, Publishers. C from Woronin; D from Pringsheim.)

The zygote is doubtless the diploid structure, but as in the majority of fresh water algae, nothing is definitely known as to the time and place of the reduction division.

The Power of Healing Wounds.—Vaucheria, as well as many other members of the Siphonales, show a remarkable capacity to heal wounds when parts of the plant are cut or injured. When a filament of Vaucheria is cut in two by a sharp instrument, the cut ends may in fifteen minutes

be closed by the formation of a cellulose wall. Masses of the contents that escape when a filament is severed may also become invested with a wall, especially if the escaped mass contains more than one nucleus. Filaments that are injured even slightly by pressure, or otherwise, will form a transverse septum at the point of injury. Or, if the injury be of greater extent in a linear direction, the entire injured portion may be divided off from the adjacent parts of the filament by cross walls. It is readily seen that this ability to repair injury or to heal wounds is of great value to the plant.

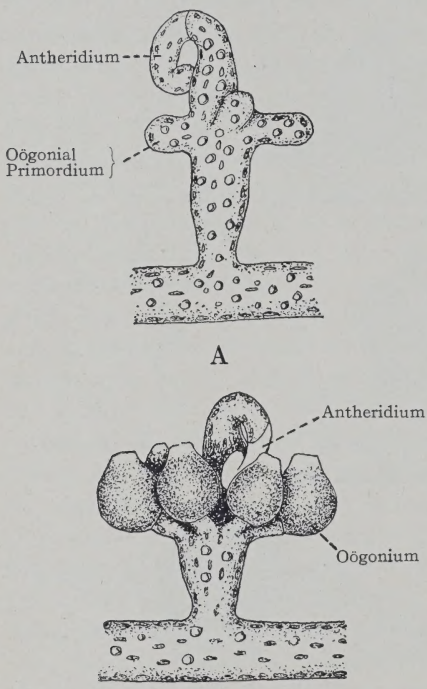


FIG. 219.—Formation of sexual organs in *Vaucheria geminata*, var. *racemosa* (Vauch.) Walz. A, the short side branch ending in the curved antheridium below which are the beginnings of oögonia. B, mature sex organs. (Adapted from Campbell's "University Textbook of Botany." By permission of the Macmillan Company, Publishers.)

Botrydium.—*Botrydium granulatum* (L.) Grev. is a multinucleate, unicellular, terrestrial plant consisting of a deep green pear-shaped part above the ground, one to two millimeters in diameter, which tapers below to a narrower portion terminating in a system of much branched, colorless rhizoids that extend into the soil (Fig. 220, A.) The part above the ground contains numerous small, rounded chloroplasts. The reserve food is in the form of an oil. Reproduction is effected by swarm spores, each having one long and one very short cilium (Fig. 220, B, C, D).

The plant is common during the summer and early autumn on moist soil, along the edges of ponds, and in cultivated fields. Following rainy weather the plant may become so abundant on clay soil in corn fields as to impart a green cast to the ground.

Protosiphon.—Associated with Botrydium in the same habitat is *Protosiphon botryoides* (Kütz.) Klebs, a small, green, rounded or globular plant, which sends down into the soil a colorless, and generally unbranched, rhizoid-like part. The chloroplast consists, however, of a parietal, net-like layer, in which starch is present as a reserve food. The plant propa-

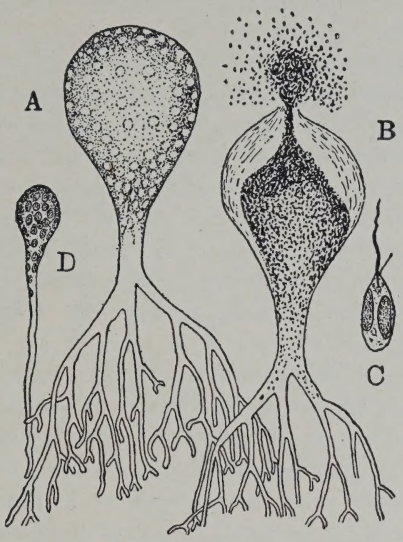


FIG. 220.—*Botrydium granulatum* (L.) Greville. A, an entire plant; B, plant producing swarm spores; C, swarm spore with one long and one short cilium; D, young plant developed from a swarm spore. (Redrawn from Kny's chart.)

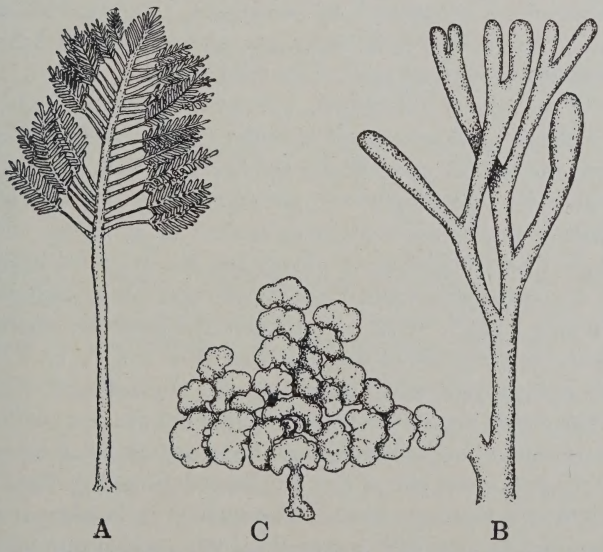


FIG. 221.—A, *Bryopsis plumosa*. B, portion of a plant of *Codium tomentosum*. C, *Halimeda opuntioides*. (A, modified from Thuret.)

gates vegetatively by division, the daughter cells sending down rhizoid-like prolongations.

Sexual reproduction is accomplished by biciliate gametes. When dried out or exposed to the sun, the cell contents separate into resting cells which become red in color. On being placed in water these develop biciliate gametes that unite to form star-shaped zygotes, which, after a period of rest, give rise directly to new plants. On moist earth the resting cells may develop directly into new plants. It is said that under some conditions the gametes do not unite but germinate directly.

Protosiphon is classed with the Protococcales by some authors.

The larger Siphonales, such as Bryopsis, Codium, Caulerpa, and Halimeda, are marine (Fig. 221, A, B, C).

Phyllosiphon.—A strange anomaly is presented by species of this genus which live as parasites within the tissues of leaves and stems of higher plants, as in the Jack-in-the-pulpit of our flora; in Europe the host is *Arisaema vulgare*, a plant related to our *Arisaema triphyllum*. Although the parasite does not penetrate the cells of the host, nor are specialized haustoria developed, it nevertheless ultimately exhausts the cells of the host.

CHARALES (CHAROPHYTA)—STONEWORTS

Of the green algae, the Charales are the most highly differentiated. They are represented, in our flora, by two genera, Chara and Nitella, which are to be found submerged in lakes, ponds, and streams, attached to the soil by means of filamentous, much-branched rhizoids.

Chara.—A species of this genus will serve as an example. Chara consists of a slender axis composed of nodes (joints) and internodes (the part between the nodes) upon which are borne at each node a circle of dwarf branches (of limited growth), consisting also of nodes and internodes. These branches are sometimes spoken of as leaves. From the nodes of these dwarf branches are developed the so-called leaflets (Fig. 223, B, *l*). From the axil of one of the dwarf branches at each node there may arise a long branch or shoot (of unlimited growth), which repeats in every detail the structure of the main axis (Fig. 222, A, *a*). From one or more of the lower nodes are developed the multicellular, filamentous rhizoids. The sexual organs are borne at the nodes of the dwarf branches, the oval or elongated oögonium being above the globular antheridium. Frequently the plants are only a few centimeters in height, but they may attain a length of a meter or more. The surface of the older parts of the plant is often coated over with a deposit of lime, which accounts for the rough surface and for the brittle character of material that has been preserved in alcohol.

*Growth and Structure.**—The main axes and branches grow from an apical cell, which in the long shoots is hemispherical in shape (Fig. 222, B). From its base, segments are cut off by transverse divisions. Each of these disk-shaped segments divides transversely into an upper cell from which a node arises, and a lower which gives rise to the central inter-

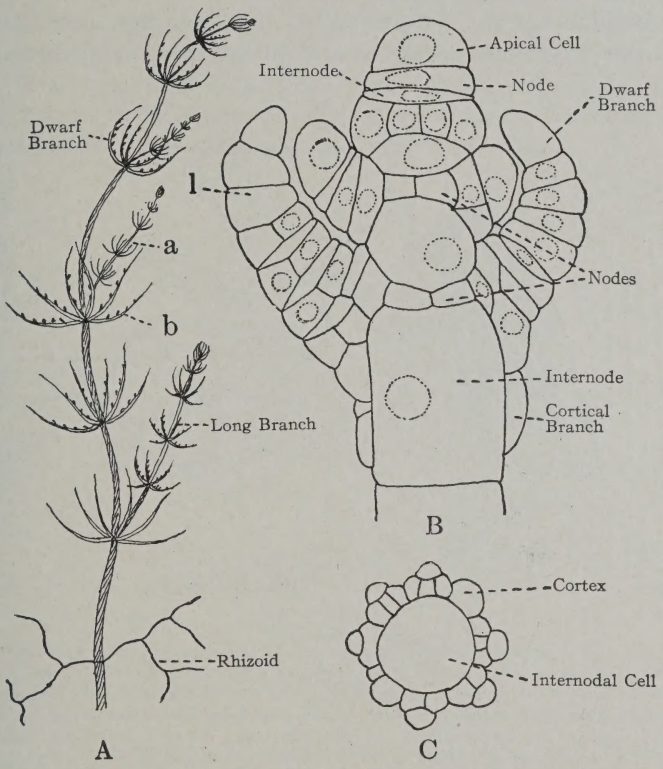


FIG. 222.—*Chara fragilis*. Habit and structure of certain vegetative parts. A, portion of plant showing long branches (*a*), dwarf branches (*b*), and rhizoids. B, longitudinal section through growing tip. C, cross section of internode, showing internodal cell and surrounding cortex. (Adapted from Campbell.)

nodal cell. The latter is incapable of further division, but it increases enormously in size, extending the entire length of the internode. The upper segment, which elongates little if any, gives rise, by vertical divisions, to a node, ultimately consisting of a transverse disk of cells.

From the nodes all lateral members—dwarf shoots, long shoots, and rhizoids—are developed. The sex organs arise from the nodes of the dwarf branches (Fig. 223, A). Each central internodal cell is finally surrounded

* Only a brief description of details is given here.

by a cellular cortex, consisting of strips or lobes, one-half of which grows downward from the upper node, and the other half coming upward from the lower node (Fig. 222, B). These two halves of the cortex meet in a zigzag line about midway between the nodes. A cross section of an internode, as in Fig. 222, C, shows the relation of the central internodal cell and the surrounding cortex. The leaflets and terminal portions of the dwarf branches are not corticated. When a long branch is formed it takes the place of one of the upward-growing lobes of the cortex.

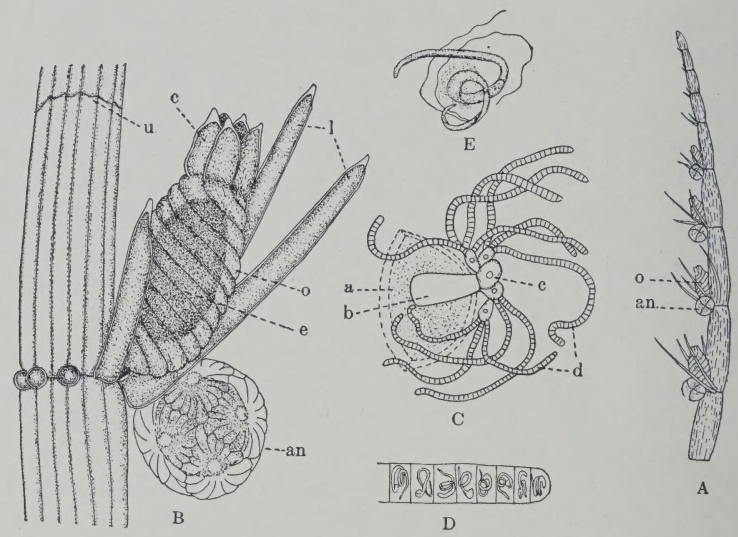


FIG. 223.—Sex organs of *Chara fragilis*. A, terminal portion of dwarf branch showing position of oögonia (*o*) and antheridia (*an*). B, node of dwarf branch with sex organs more highly magnified; *o*, oögonium; *c*, crown of oögonium; *e*, egg, *an*, surface view of antheridium; *l*, leaflets; *u*, line where ascending and descending cortical lobes meet. C, part of the antheridium as seen when the organ is carefully opened; *a*, a shield cell; *b*, manubrium; *c*, capitulum, to which are attached secondary capitula; *d*, sperm-bearing filaments. D, part of filament showing sperms in the cells. E, a sperm. (Figures adapted; A, Strasburger, Macmillan Co.; B, from Sachs; C and D, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. E, from Mottier.)

The rhizoids grow also by means of apical cells. As stated above, they are formed from the lower nodes of the axis. The rhizoids are often spoken of as roots.

Vegetative Propagation.—Any mature node is capable of developing a shoot and rhizoids, thus producing a new plant. This may readily be demonstrated under experimental conditions by selecting a portion of the main axis consisting of two or more nodes and thrusting one of the nodes into the sand or soil in the bottom of the aquarium. Special bud-like

structures are sometimes developed from the older nodes and on the rhizoids.

Sexual Reproduction.—The sex organs of the Charales are the largest and most complex among the algae. They spring from the nodes of the dwarf branches (Fig. 223, A). The mature oögonium of Chara consists of a large oval or elliptical egg surrounded by a cover of five tubular cells, which make two or more spiral turns around it. From the upper end of each of the tubular cells a short cell is cut off, the five constituting the crown of the oögonium (Fig. 223, B, *c*). When the egg is ready for fecundation the spirally twisted cells separate slightly below the crown, forming five clefts through which the sperms may enter.

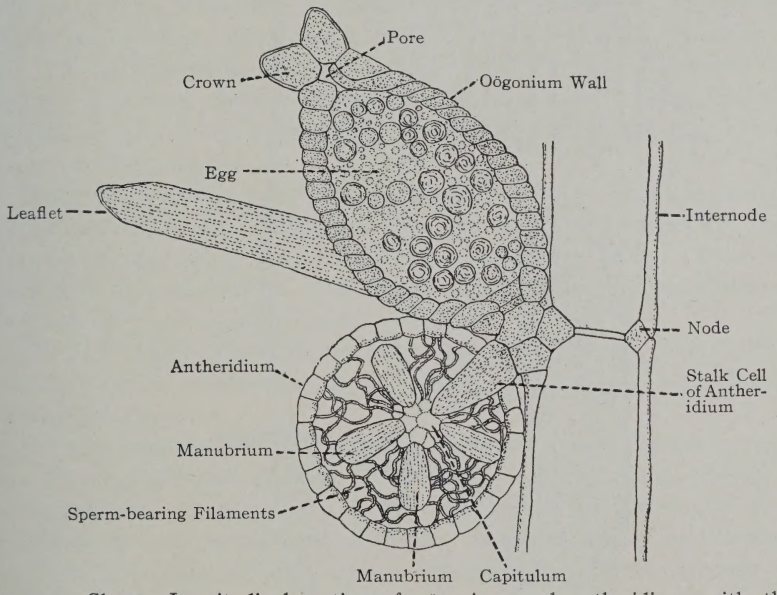


FIG. 224.—Chara. Longitudinal section of oögonium and antheridium, with the node at which they are borne. (Strasburger, Macmillan Co.)

The mature antheridium is globular in form and red in color, owing to a change of the green chloroplasts to red (Fig. 223, B, *an*). The vegetative framework of the antheridium consists of twenty-five cells. The eight triangular peripheral cells, four at each pole, are known as the "shields." The outer cell wall of each shield is marked by folds which radiate from the center and impart the very characteristic appearance to the surface of the antheridium. From the center of each shield there extends inward a large cyclindrical cell, the *manubrium*. Each manubrium bears at its inner end a rounded cell, the *capitulum*, and each capitulum cuts off one or more secondary capitula. From the capitula

grow out long, slender sperm-bearing filaments composed of numerous short cells. The four basal shields of the antheridium are attached to a large stalk-like cell which projects into the cavity of the antheridium, its inner end meeting the capitula (Fig. 224). Fig. 223, C represents one

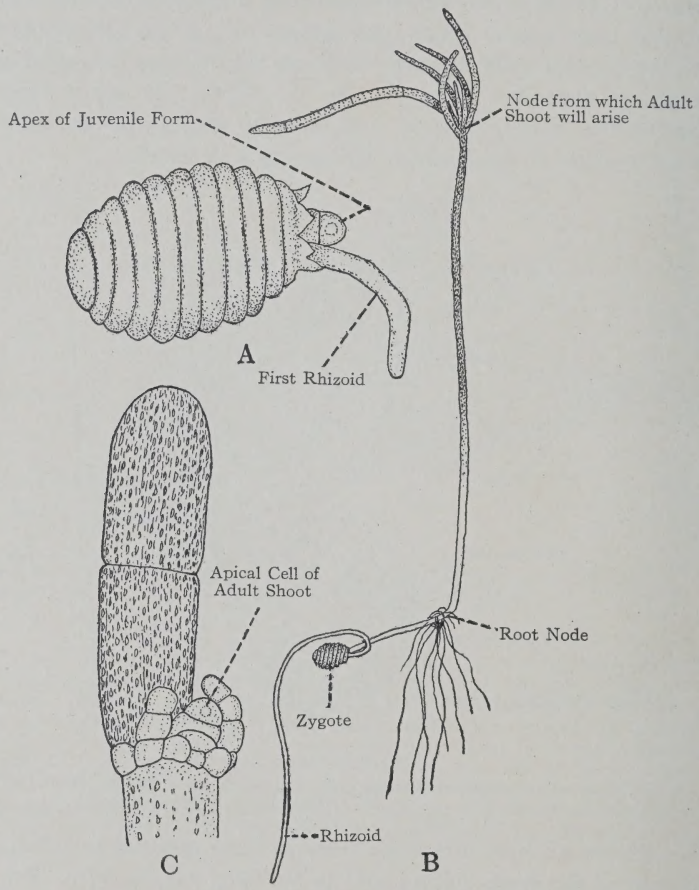


FIG. 225.—Chara. Germination of the zygote, and juvenile form (pro-embryo). A, germinating zygote; B, proembroy; C, distal end of proembryo. (A, C, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. B, from Pringsheim.)

shield with a manubrium and its capitulum. Attached to the secondary capitula are a number of spermogenous filaments, *d*.

The spermogenous filaments are coiled up in the spaces between the manubria (Fig. 224). From each cell of the filaments one sperm is

formed. The sperm is a spirally coiled body, consisting of a nucleus and an especially differentiated part of the cytoplasm in the form of a thread or band. This differentiation, known as the *blepharoplast*, bears two long cilia (Fig. 223, E). The nucleus occupies the middle part of the sperm, while the blepharoplast extends its entire length. The posterior end of the blepharoplast is thicker and usually ends bluntly.

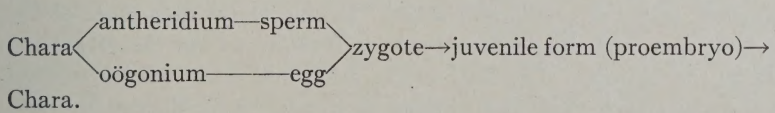
Fecundation, Zygote, and Proembryo.—When the antheridium is mature the shields separate and the sperm-bearing filaments are exposed to the water. Each sperm escapes through an opening in the wall of the cell that bore it. The sperm enters the oögonium through one of the clefts beneath the crown and unites with the egg. The zygote passes into the resting stage and remains within the oögonium, which may become red in color. The oögonium with the enclosed zygote is a kind of fruit. It falls from the plant and sinks to the bottom of the pond or stream. The outer walls of the spiral cortical cells may decay, leaving the hardened inner walls standing out from the surface like the threads of a screw (Fig. 225, A).

On germination the zygote produces first a small filamentous *proembryo*, a juvenile form of the Chara plant (Fig. 225, B). This proembryo consists of a primary rhizoid and a small shoot having two nodes. From the lower node rhizoids develop, and from the upper arises the adult form of the plant as a lateral bud (Fig. 225, C).

The diploid structure in Chara is the zygote. If the reduction division occurs during the germination of the zygote, the resulting Chara plant is the haploid structure.

In one species of Chara, *C. crinita*, it has been claimed for many years that the egg develops without fecundation, a phenomenon known as *parthenogenesis*. If the egg of this species possesses the single number of chromosomes, true parthenogenesis occurs, this being one of the few cases of such in the plant kingdom. But if the egg in this species contains the double number of chromosomes (no reduction having taken place), the phenomenon is not parthenogenesis, but *apogamy*.*

A diagram of the life cycle of Chara may be written as follows:



* Parthenogenesis consists in the development of one gamete (here an egg) without union with another gamete. A gamete contains the single number of chromosomes. If the cell which seems to be an egg contains the double number of chromosomes, it is not a gamete; it cannot be fecundated, and its development constitutes what is properly known as *apogamy*. It may be reasonably questioned, therefore, whether such a thing as parthenogenesis occurs in the plant kingdom.

Nitella.—Another representative of the Charales commonly met with in our flora is Nitella. Having the same structural plan of nodes and internodes, it bears a striking resemblance to Chara. It differs from Chara in lacking a cortex, the large internodal cell being naked (Fig. 226, A). The oögonia and antheridia are similar to those of Chara, but the antheridium is borne above one or more oögonia, at the same node, and

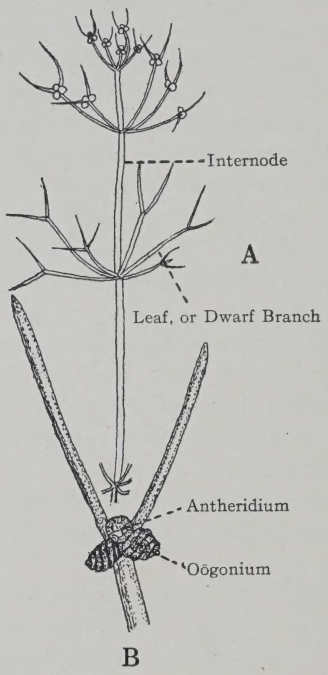


FIG. 226.—*Nitella flexilis*. A, a fertile branch; B, leaf with two leaflets, and bearing two oögonia and an antheridium. (From Sachs.)

the crown is composed of ten cells in two tiers instead of one tier of five cells (Fig. 226, B).

Mineral Deposit.—Chara often forms dense and extensive growths in the shallow water of ponds and lakes. During the winter most of the plant body dies, and the detritus resulting from decay and disintegration settles to the bottom. The limy incrustation and other mineral matter form a deposit each year, and in some such manner our deposits of marl may have been built up in past ages.

CHAPTER XIII

THALLOPHYTA—PHAEOPHYCEAE—BROWN ALGAE

The brown algae, the larger forms sometimes commonly called "kelps" or "rockweeds," are nearly all marine plants. They occur on all seacoasts, but attain their highest development in the cooler seas. They vary greatly in size, form, and structure, ranging from simple filaments to very large, massive structures with highly differentiated tissues. The giant kelp (*Macrocystis pyrifera*), which is the largest alga known to science, is said to attain a length of from 200 to 300 meters.

The characteristic brown color is due to the presence in the chloroplast of *fucoxanthin*, a pigment similar in chemical composition to xanthophyll. Brown algae vary in color from a deep brown to various shades of olive green; the characteristic pigment is always present, however. The large forms are of a tough, leathery texture, and are firmly anchored to the rocks or other objects by means of large holdfasts. Many are always submerged, but some, as in the case of Fucus, grow between high and low tides, so that the plant body is periodically exposed to the air at regular intervals.

There are three well defined larger subdivisions of the brown algae: Phaeosporales (Phaeosporeae), Fucales (Cystosporeae), and Dictyotales. As an example for more detailed presentation we shall select a species of Fucus.

FUCALES

FUCUS

Form and Structure.—The thallus, or plant body, consists of a flat, leathery, ribbon-like, dark brown structure traversed by a midrib. The midrib is continued downwards into a rounded and somewhat cylindrical stalk, which ends below in an organ of attachment, the holdfast (Fig. 227, A). The branching is dichotomous. Here and there may be present large inflations, air vesicles, which help buoy up the plant in the water. These are sometimes grouped in pairs. Scattered over the flattened part of the plant, on both sides of the midrib, are numerous small dots (Fig. 227, A). At the center of each dot is a pore, which leads into a cavity known as a *cryptostoma* (Fig. 227, B).

In specimens bearing sex organs the ends of certain branches are enlarged and marked by numerous conical protuberances (Fig. 227, A). In the center of each protuberance is a small pore leading into a relatively large flask-shaped cavity, the *conceptacle*, in which one or both kinds of sex organs are present.

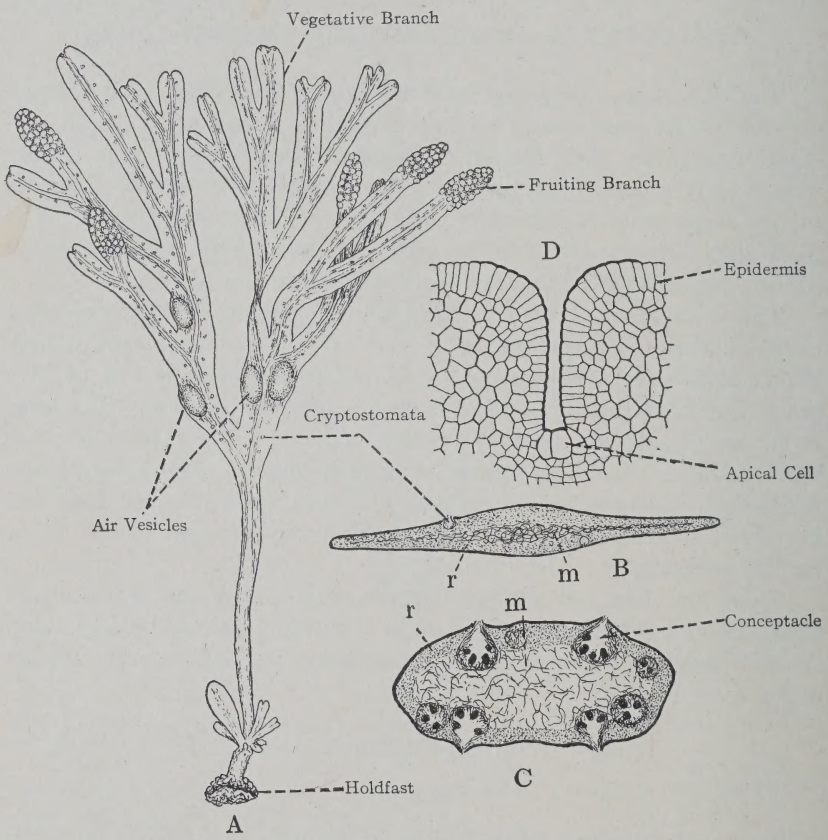
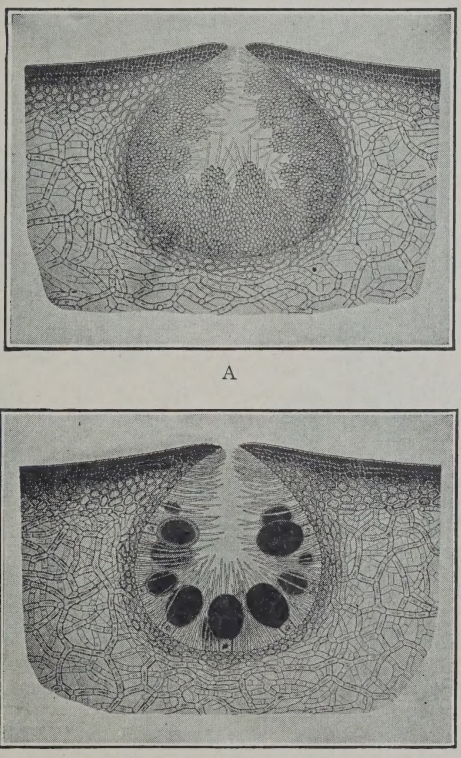


FIG. 227.—Fucus. A, portion of plant showing habit; B, diagram of cross section of thallus; *r*, outer rind; *m*, loose inner pith, or medulla. C, cross section of a fruiting tip; D, longitudinal section of a growing point taken at right angles to the flat surface, showing the pit, or depression, at the bottom of which is the apical cell. (D, from Kny's chart.)

In cross section, the structure of the thallus is seen to consist of a firm rind, and a soft pith, or medulla (Fig. 227, B). The rind is made up of small, closely arranged, isometric cells. The outer layer of these, which can be traced quite to the growing point, is the epidermis. The pith is composed of large cylindrical cells so placed together as to form a

sort of network (Fig. 227, B, and Fig. 228). A copious mucilaginous substance present throughout the plant is derived from the outer surfaces of the cell walls.

Apical Growth.—The growing point of each branch of the thallus ends in an apical cell, somewhat rectangular in section, situated in a small depression at the tip of the branch (Fig. 227, D). From this apical cell all other parts of the branch are primarily derived. The successive



A

B

FIG. 228.—*Fucus vesiculosus.* Vertical sections through male (A) and female (B) conceptacles. (From Kny's chart, after Thuret.)

divisions of the apical cell take place in such manner that cells are cut off from the four lateral faces and from the inner, or posterior, end. The true epidermis and other parts of the thallus can readily be traced to the apical cell (Fig. 227, D). When the growing point branches such branching is due to a division of the apical cell into two nearly equal cells, each of which becomes the apical cell of a new branch. Dichotomous branching, which is so characteristic of Fucus, arises in this manner.

Reproduction.—Asexual reproduction by means of spores is unknown in the Fucaceae. Some of the Fucaceae, such as *Fucus vesiculosus* and species of Halidrys, are dioecious; others, such as *Fucus fastigiatus*, are monoecious. The oögonia are borne in rounded or flask-shaped cavities, *conceptacles*, aggregated at enlarged club-shaped ends, as in Fucus, or on special branches as in Sargassum (Fig. 231).

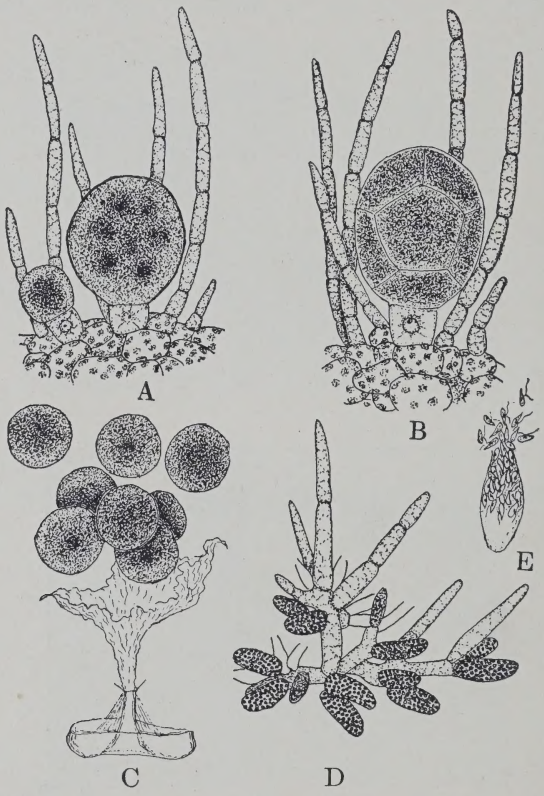


FIG. 229.—Sex organs of *Fucus vesiculosus*. A, two stages in the development of the oögonium. B, oögonium in which the eight eggs have been formed. C, eggs escaping from an oögonium. D, branched filaments from the male conceptacle, bearing antheridia. E, mature antheridium with sperms escaping. (From Thuret.)

Antheridium.—Fig. 228, A, represents a male conceptacle. The antheridia (Fig. 229, D) are small oval or rounded cells borne at the ends of short branches arising from the inner wall of the conceptacle. At first the antheridium is a single cell. Its nucleus undergoes many repeated divisions, and finally cell division takes place, resulting in a large number of naked, biciliate cells, the sperms. When mature, the sperms are discharged into the water. Each is a pear-shaped cell provided with two

laterally inserted cilia, one longer than the other, and an orange-red pigment spot (Fig. 229, E).

Oögonium.—Fig. 228, B represents a female conceptacle. The oögonia arise also on short branches from the inner wall of the conceptacle. The young organ consists of a short basal stalk cell and a large terminal cell which bears the eggs. By three successive divisions the nucleus of this cell gives rise to eight nuclei, and the cell then divides into eight eggs (Fig. 229, A, B). At maturity the wall of the oögonium is dissolved, and the dark brown, non-motile eggs are discharged through the ostiole into the water (C).

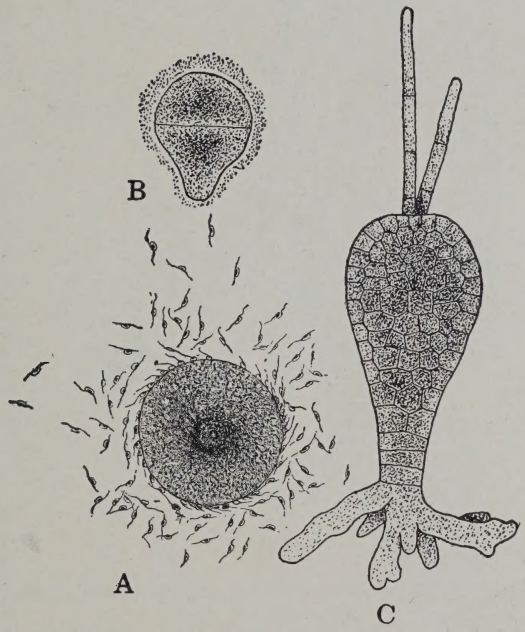


FIG. 230.—*Fucus vesiculosus.* A, egg to which sperms are attached. B, germinating zygote. C, young plant developing from zygote. (From Thuret.)

Fecundation.—Certain phenomena of fecundation may be readily observed at the seaside laboratory. Fruiting ends of branches from which the gametes are being discharged are placed in dishes of sea water, the male and female branches being kept in separate dishes. If the eggs and sperms are properly brought together in a dish, or in a suitable mount for microscopic observation, some of the eggs will soon be seen rolling slowly through the water. Numerous sperms attach themselves to the surface of the egg. Each attaches itself by one cilium, while the other lashes the water. By this means each sperm maintains a circular

or gyratory motion about its point of attachment. The movement is in the clockwise direction. By the combined action of all the sperms the egg is rolled slowly through the water (Fig. 230, A). Very soon a sperm enters the egg, and all the other sperms depart. The sperm and egg nuclei unite in a short time, and the zygote begins to grow without a period of rest. In the development of the new plant, the zygote divides into two cells, the lower one giving rise to the holdfast and the upper to the body of the plant (Fig. 230, B, C).

Haploid and Diploid Structures.—It has been found that the first mitosis in the oögonium of Fucus is a reducing division. It is assumed

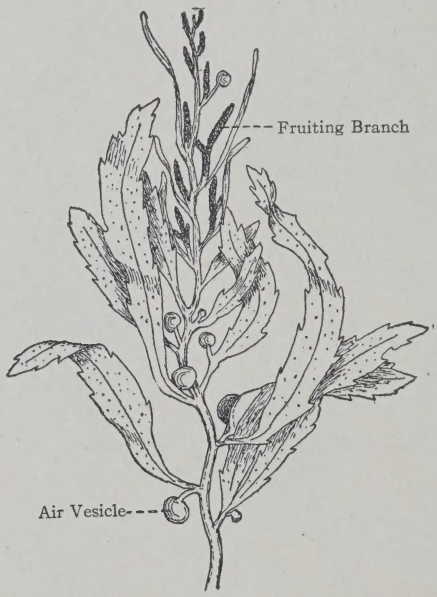


FIG. 231.—Sargassum. Habit sketch showing air vesicles and fruiting tips containing sex organs. ×1.

that a reducing division takes place also in the development of the antheridium. Eggs and sperms have the single number of chromosomes, and they alone represent the haploid structure, while the Fucus plant, whose cells have the double number of chromosomes, is the diploid structure.

Among other Fucales may be mentioned Sargassum, Halidrys, Ascophyllum. Sargassum is usually found floating in extensive areas in certain parts of the ocean far from the land, and because of this fact the plant constitutes the characteristic feature of the Sargasso Sea (Fig. 231). These floating masses of seaweed serve as a shelter for a great variety of marine animals, small fishes even being found among them.

In certain Fucales fewer than eight eggs are formed in the oögonium. In Halidrys one egg is developed; in other genera two or four are formed. In all forms that have been carefully studied eight nuclei are present in the oögonium although eight eggs may not be developed.

PHAEOSPORALES

Among the Phaeosporales are included some of the smallest and simplest Brown Algae, as well as the largest and most complex.

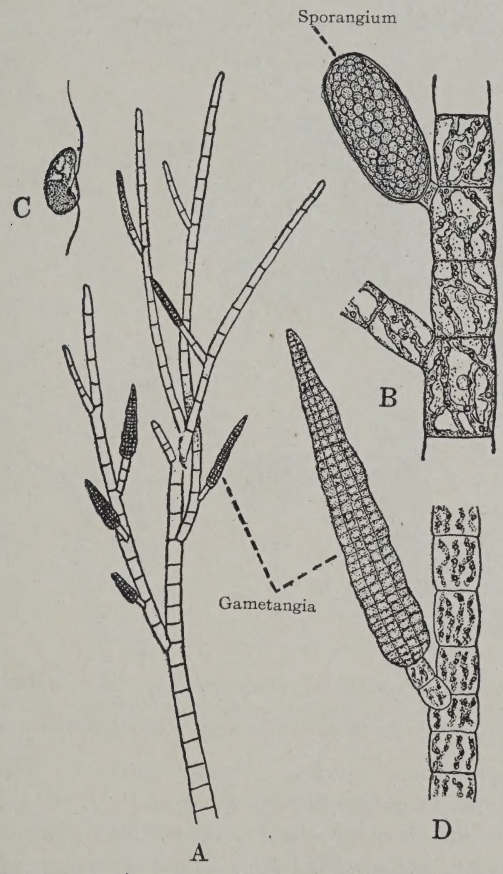


FIG. 232.—Ectocarpus. A, portion of plant showing habit; B, part of branch with a sporangium; C, Swarm spore; D, similar part of a plant with gametangium. (C, after Oltmanns.)

One of the best known simpler forms is Ectocarpus, which consists of simple branched filaments (Fig. 232, A). The large forms are represented by Macrocystis, Postelsia (the Sea Palm), Laminaria (Fig. 234, A), and numerous others.

Asexual Reproduction.—To illustrate both sexual and asexual reproduction in this group we may select *Ectocarpus siliculosis*. Asexual reproduction is accomplished by swarm spores, which are pear-shaped cells, each bearing two laterally inserted cilia, an eye spot, and a chloroplast (Fig. 232, C). They are borne in what have long been known as *unilocular sporangia* (Fig. 232, B). In such a sporangium, which consists of a single cell, the contents divide successively into numerous cells which may not be separated by cell walls. These naked cells escape as swarm spores and develop directly into individual plants.

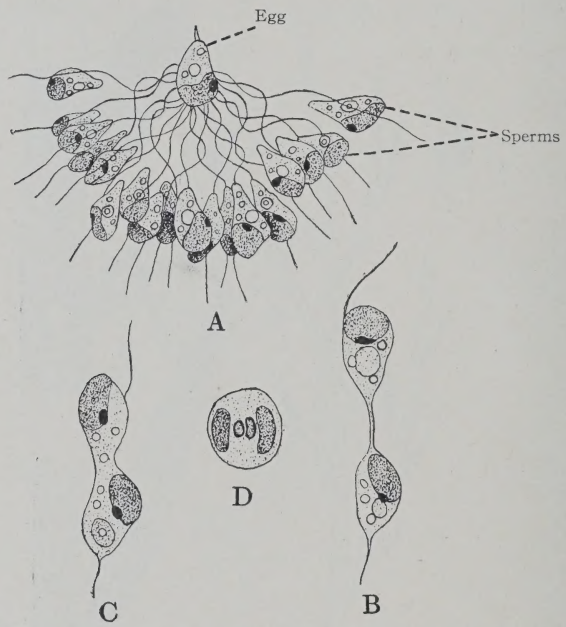


FIG. 233.—Union of gametes in *Ectocarpus siliculosis*. A, egg to which are attached a large number of sperms. B, C, egg and one sperm uniting. D, zygote just before fusion of the nuclei, which are lying side by side. (From Berthold and Oltmanns.)

Sexual Reproduction.—Sexual reproduction is accomplished by motile gametes, which escape into the water and unite to produce zygotes. The gametes are similar in structure to the swarm spores, though smaller. They are formed in the so-called *plurilocular sporangia*, which in reality are gametangia (Fig. 232, D). The initial cell of a gametangium divides into numerous small, cubical cells, which are separated by cell walls. The contents of each of these cells form a motile gamete, which escapes into the water. In some species the gametes are unequal in size, the larger being eggs, and the smaller, sperms. It is also probable that the two sorts of gametes are borne in different gametangia. In fecundation,

when observed in a hanging drop, the female gamete, as a rule, comes to rest first, and a number of sperms assemble about it. The sperms attach themselves by means of the longer cilium, as shown in the familiar illustration of Berthold (Fig. 233, A). One of the sperms now approaches the egg by a sudden contraction, and unites with it, while the others withdraw.

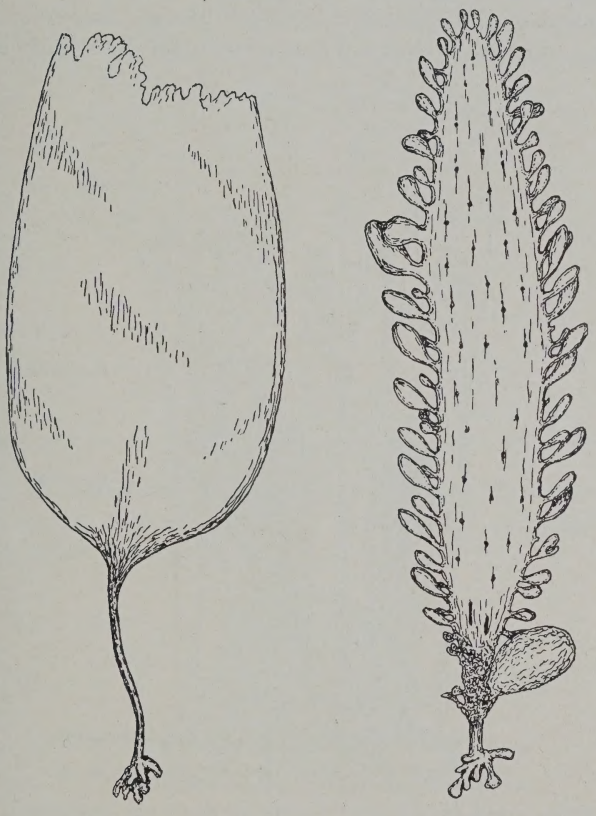


FIG. 234.—A, small plant of Laminaria. B, a young plant of *Egregia menziesii* Aresch. (From specimens collected by W. R. Shaw, at Point Lobos, California. × ⅔.)

The two gametes then fuse to form the zygote. The chloroplasts do not unite (Fig. 233, B, C, D). The zygote germinates directly to form a new plant.

Haploid and Diploid Individuals.—For many years only the asexual form of reproduction was known in the large Phaeosporales, such as Laminaria, the sporangia being produced in large aggregations called *sori*

(Fig. 235). In recent years it has been reported that these swarm spores do not develop into the large plant as we know it, but, on the contrary, give rise to very small, filamentous sexual plants, which are dioecious and bear very small antheridia and oögonia. The sperms and eggs escape into the water and form zygotes, which develop directly into the large structure known as Laminaria (Fig. 234, A).

In Laminaria, and probably in other genera, therefore, the large massive plant producing swarmspores constitutes the diploid individual,

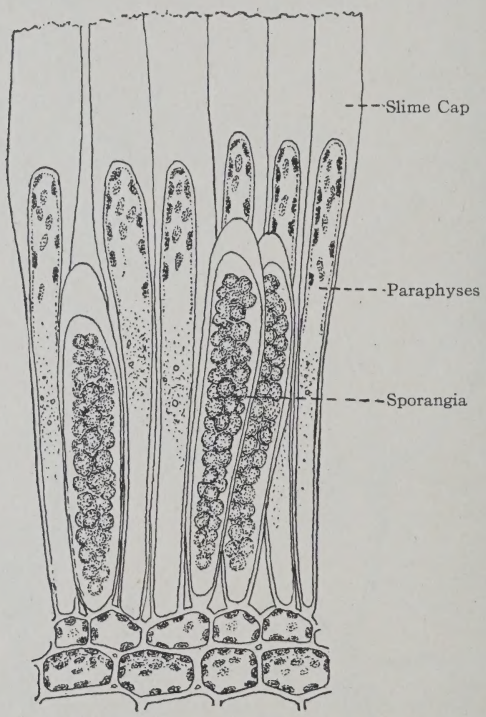


FIG. 235.—Section through a part of a sorus of *Laminaria saccharina*. (From Oltmanns; after Klebs.)

while the small sexual plants mentioned are the haploid individuals. It is highly probable also that the plants bearing the swarm spores in Ectocarpus are the diploid individuals, and those producing the gametes are the haploid individuals. In these plants the number of chromosomes has not been determined.

DICTYOTALES

Because of its resemblance to certain red seaweeds in the method of asexual reproduction, *Dictyota dichotoma* is of special interest. It consists

of a small, dark brown, flat, ribbon-like plant, dichotomously branched (Fig. 236).

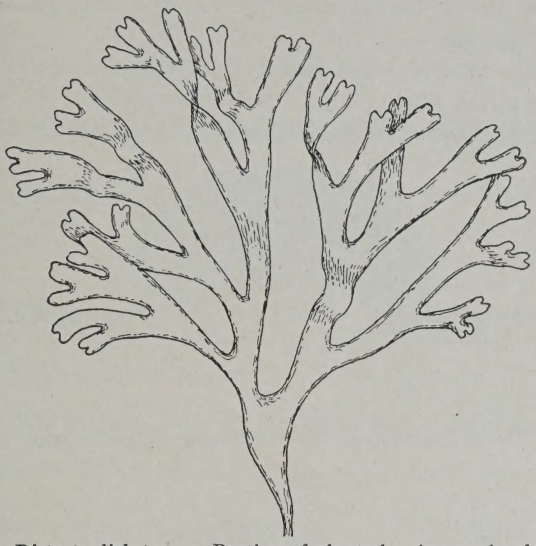


FIG. 236.—*Dictyota dichotoma.* Portion of plant showing mode of branching.

Asexual Reproduction.—It reproduces asexually by means of large, non-motile spores, termed *tetraspores*, because four are produced in a sporangium, a *tetrasporangium* (Fig. 237).

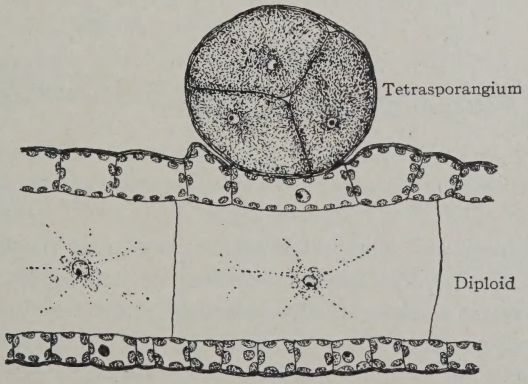


FIG. 237.—*Dictyota dichotoma.* Section of the thallus with tetrasporangium, showing three of the four spores.

Sexual Reproduction.—This is accomplished by the union of highly differentiated eggs and sperms. The oögonia are produced in clusters, one egg to the oögonium (Fig. 238, A). The eggs are large, non-motile

cells, which escape from the oögonia before fecundation. The sperms, which are motile, are produced in large numbers in antheridia, which are also aggregated in clusters (Fig. 238, B). As in Fucus, fecundation takes place in the open sea.

Haploid and Diploid Individuals.—It has been ascertained that the plant bearing tetraspores contains the double number of chromosomes, and that the reduction division takes place in the first nuclear division in

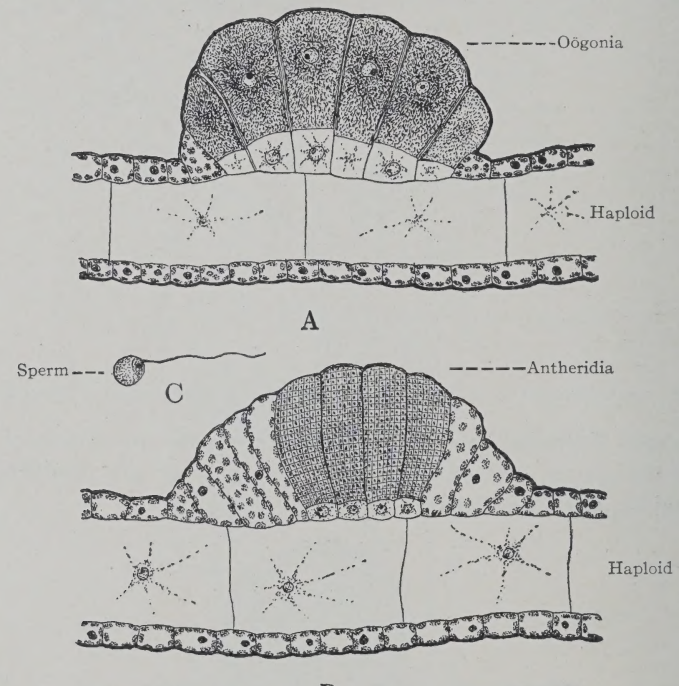


FIG. 238.—Sex organs of *Dictyota dichotoma*. A, sections of thallus with group of oögonia. B, group of antheridia. C, a sperm. (C, from Williams.)

the tetrasporangium. The tetrasporic plants are consequently the diploid individuals. The plants bearing the antheridia and oögonia contain the single number of chromosomes; they are the haploid individuals. One complete life cycle of Dictyota embraces, therefore, two similar but separate and independent individuals, namely, the haploid, represented by the individual bearing eggs and sperms, and the diploid, by those that bear the tetraspores.

CHAPTER XIV

THALLOPHYTA—RHODOPHYCEAE—RED ALGAE

The Red Algae owe their name to the characteristic red color possessed by the vast majority of the group. All are not red in color, however. Some, like Batrachospermum and Lemanea, for example, which occur in fresh water, are of a bluish green or dark olive green color. In marine forms, colors from a pale yellow to a dark purple occur. The bright red color is due to the presence of a red pigment, *phycoerythrin*, contained in the chloroplast along with chlorophyll. Phycoerythrin is soluble in rain water, imparting to the solution a rose-red color, which, owing to fluorescence, appears greenish yellow in reflected light.

In structure the Red Algae vary from delicate and almost microscopic filaments, branched or unbranched, to a larger, flat, and somewhat firm, leathery thallus. Some are strongly incrusted with lime, resembling coral-like structures (Corallina, Amphiora).

In the vast majority the chloroplasts are usually in the form of small oval disks, several in each cell. Generally, the cell walls show a tendency to become gelatinous, and the intercellular gelatinous substance often becomes so great that the cells appear to be imbedded in it. As a rule, cytoplasmic connections extend from cell to cell.

The red pigment in the Red Algae and the brown in the Brown Algae seem to be associated with light as the source of energy in the process of photosynthesis.

Batrachospermum.—As an example for a more detailed consideration, we shall select Batrachospermum, which may be found in clear, cool streams in Indiana. The whole plant consists of a juvenile form, made up of simple, branched filaments, and the adult form, the Batrachospermum (Fig. 239, A). The adult form, or part, consists of an axial row of cells, ending in an apical cell, and a complex system of branches. From the upper end of each cell of the axial row is borne a whorl, or circle, of short branches of limited growth, composed of rounded or cylindrical cells constricted at the ends. Each branch bears some resemblance, therefore, to a row of beads or necklace. These dwarf branches are in turn branched, so that the whorl constitutes a dense *glomerule*. In fruiting specimens the spore fruits, *cystocarps*, appear, under low magnification, as dense, opaque masses among the branches of the glomerules. In the younger parts

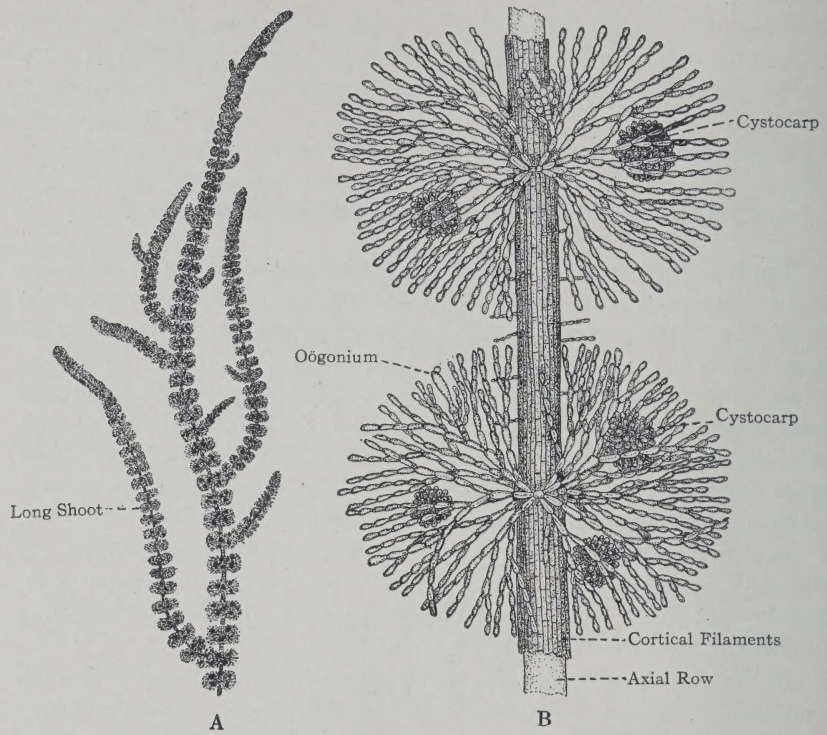


FIG. 239.—Batrachospermum. A, sketch showing habit of the plant. B, portion of long shoot with two glomerules of dwarf branches.

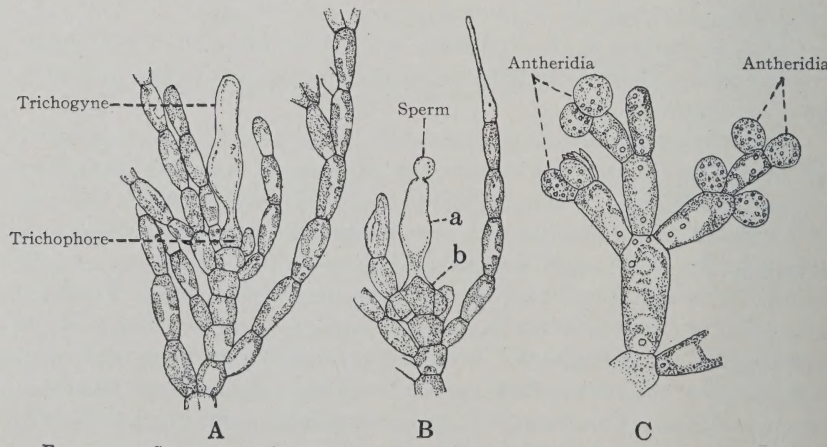


FIG. 240.—Sex organs of *Batrachospermum moniliforme*. A, part of a dwarf branch ending in an oögonium. B, after fecundation; *a*, the club-shaped terminal part, the *trichogyne; b*, the flask-shaped basal part, the *trichophore*. C, branch bearing antheridia. (A, B, Strasburger, Macmillan Co.)

of the plant the whorls of branches are so close together that they conceal the central axis completely.

In addition to the dwarf branches, long branches are developed monopodially. These repeat in every detail the structure of the main axis (Fig. 239, A). The long branches, or shoots, arise from basal cells of the dwarf branches.

In older parts of the shoot the axial row of cells is covered by multicellular filaments, which may adhere laterally to form a sort of cortex. These cortical filaments spring also from the basal cells of the dwarf

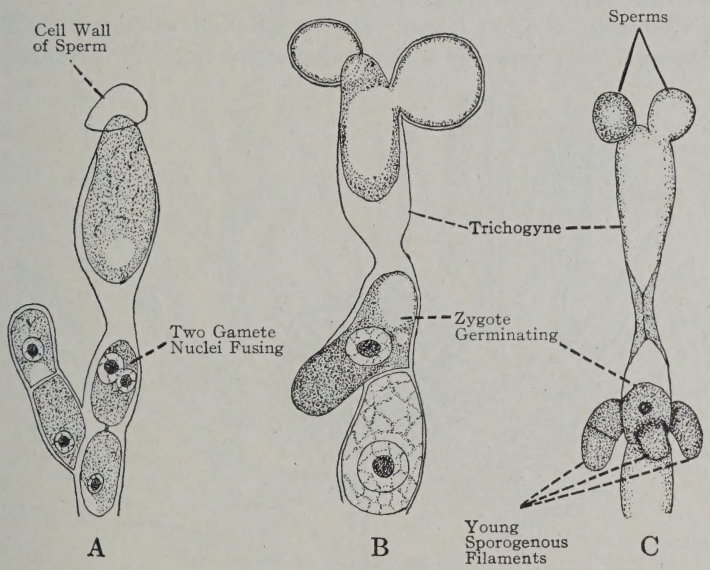


FIG. 241.—Batrachospermum. Fecundation and early stages in the formation of the cystocarp. A, fusion of egg and sperm nuclei in the trichophore. B, zygote germinating; beginning of the first sporogenous filament from trichophore. C, three young sporogenous filaments sprouting out from the trichophore. (A and B, *B. boryanum*, after Osterhaut; C. *B. moniliforme*.)

branches (Fig. 239, B). In some species, slender branches spring from the cortical filaments, giving the axis between the glomerules a hairy appearance under a low magnification. The cells of the entire plant are covered with a coat of colorless slime.

Sexual Reproduction.—The antheridia consist of single cells borne at or near the distal ends of the branches of the glomerules (Fig. 240, C). Each bears a single non-motile sperm, which escapes into the water as a naked cell. The oögonia are borne at the ends of certain branches in the glomerules (Fig. 240, A, B, *a*, *b*). Each is a single cell with a constriction near the lower end. The flask-shaped basal part is called the *trichophore*

(*b*), and the larger, elongated, club-shaped terminal part is the *trichogyne* (*a*). The nucleus and cytoplasm in the basal part constitute the egg.

Gravity and the movement of the water probably bring the sperm, or sperms, in contact with the end or side of the trichogyne, to which they adhere. When the sperms are found adhering to the trichogyne they possess a cell wall (Fig. 240, B). By dissolution of the cell walls an opening is formed between the sperm and the trichogyne. The contents of the sperm now pass into the trichogyne, and the opening in the latter is closed. The sperm nucleus passes down into the trichophore and fuses with the egg nucleus (Fig. 241, A).

The Cystocarp, or Spore Fruit.—The constriction between trichophore and trichogyne soon closes by a thickening of the cell wall. Neither the

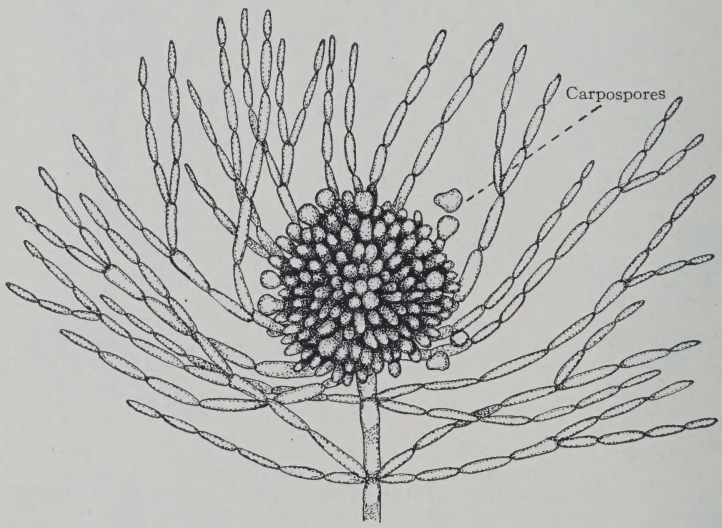


FIG. 242.—*Batrachospermum moniliforme.* Mature cystocarp. The cystocarp, borne at the end of a dwarf branch of the glomerule is surrounded by numerous secondary branches.

unfertilized egg nor the zygote rounds up or separates from the wall of the oögonium. The zygote begins germination at once. From it there grow out in all directions numerous short filaments, each of which ends in a spore, called a *carpospore.* These filaments are spore-bearing, or *sporogenous*, filaments, and all together form a cystocarp (Fig. 242).

The sporogenous filaments are developed as follows: at one side of the trichophore after fecundation a bud-like protuberance is sent out. The nucleus of the zygote divides, one daughter nucleus remaining in the trichophore, the other passing into the protuberance, after which the division of the cell is completed (Fig. 241, B). This cell thus formed

elongates and divides again, and the process is repeated until the completion of the sporogenous filament. The nucleus remaining in the tricho-

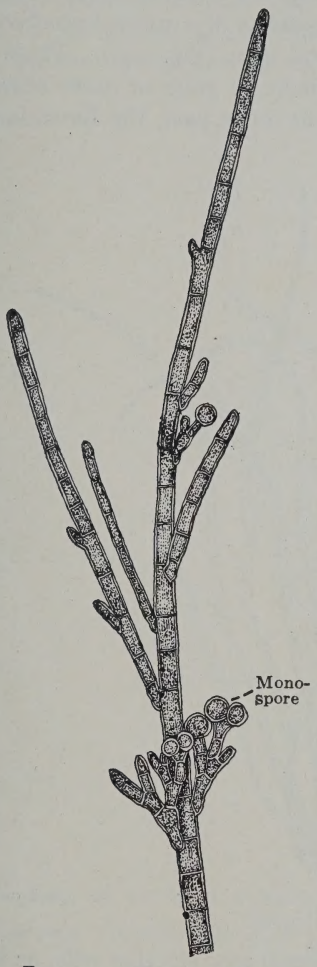


FIG. 243.—Branch of juvenile form of Batrachospermum.

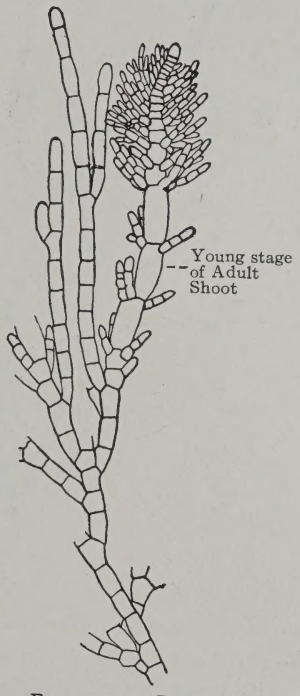


FIG. 244.—*Batrachospermum ectocarpum.* Juvenile branch with a young shoot of the adult form. (Adapted from Sirodot.)

phore again divides, and another sporogenous filament is produced as above described (Fig. 241, C). The process is continued until the entire cystocarp is developed. It will be seen that the nuclei of the sporogenous

filaments and the carpospores are descendants of the nucleus of the zygote.

The Juvenile Form.—Presumably the juvenile form originates primarily from the carpospores. It consists of a much branched filament, resembling Cladophora in structural plan (Fig. 243). These filaments grow in dense tufts attached to blades of grass or other objects in the water. From this juvenile form, the adult part, the Batrachospermum, arises as a special branch.

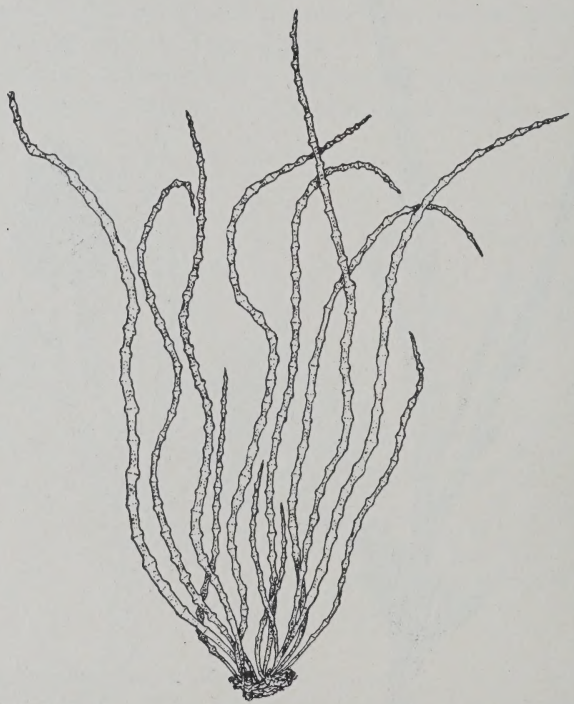


FIG. 245.—Lemanea. Several shoots attached to a bit of limestone. (Slightly enlarged.)

The juvenile form develops asexual reproductive cells, or *monospores*, borne singly at the ends of short branches (Fig. 243). In Fig. 244 is shown the manner in which the adult shoot, Batrachospermum, arises as a massive branch from the juvenile filament.

The following is a diagram of the life cycle of Batrachospermum:

Batrachospermum < oögonium—egg / antheridium—sperm > zygote→cystocarp→ carpospores→juvenile form→Batrachospermum (adult form).

Lemanea, as shown in Fig. 245, is a slender, tubular thallus with node-like enlargements at regular intervals. At each enlargement may be seen one or more openings through which the sperms enter. The oögonia are borne in the interior of the thallus, the antheridia on the exterior. Lemanea has also a filamentous juvenile stage from which the adult

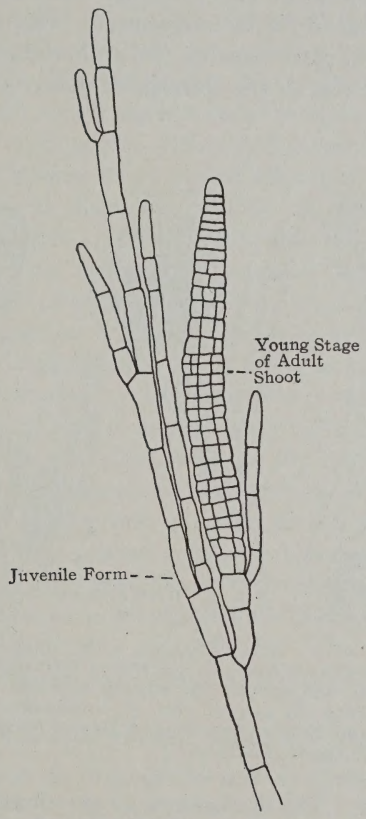


FIG. 246.—Lemanea. Juvenile form with young stage of adult shoot arising as a branch.

shoots arise as branches. The origin of an adult shoot from the juvenile stage is shown in Fig. 246.

Other Types of Red Algae.—As in Dictyota and certain Phaeosporeae, the complete life cycle of some of the Red Algae is known to consist of two distinct individual plants. One of the individuals bears tetraspores, and is called the tetrasporic plant, or the diploid individual; the other bears cystocarps and carpospores and is known as the haploid plant. The two plants may resemble each other closely.

The above statement may be made clear by means of a concrete case, such as that afforded by Polysiphonia. Fig. 247, B represents a portion of the haploid plant bearing a cystocarp. Here the cystocarp is not naked as in Batrachospermum, but surrounded by an urn-shaped protective covering, provided with an opening at the top through which the carpospores escape. Apart from the covering, these cystocarps arise in a manner similar to that in Batrachospermum. Fig. 247, D, is the end of a branch of a haploid plant bearing two antheridia, *a*. The carpospores on germination give rise to the tetrasporic plant, a portion of which is

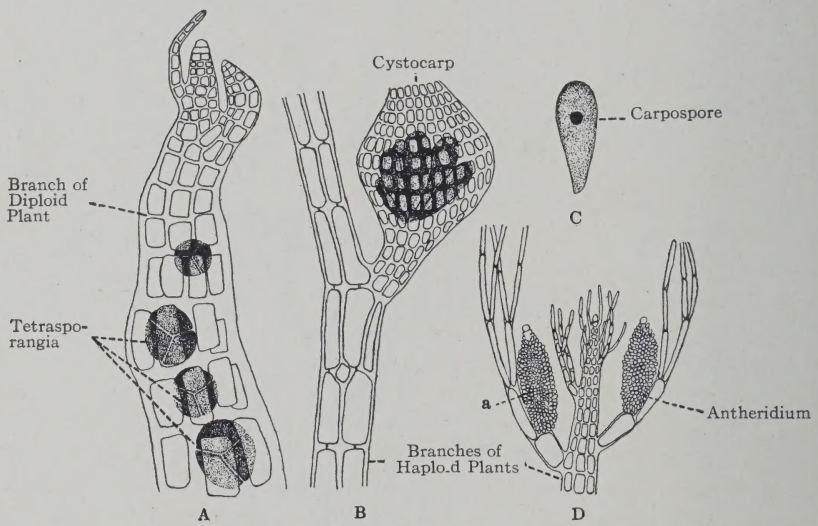


FIG. 247.—*Polysiphonia violacea*. A, tip end of tetrasporic plant, showing tetrasporangia, each with its four spores. B, portion of haploid plant bearing an urn-shaped cystocarp, enclosing the carpospores. C, a carpospore. D, branch with two antherida, *a*. (B, C, and D from Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

shown in Fig. 247, A. The tetraspores, on germination, give rise, in turn, to the haploid individuals.

Summary.—1. In habit and structure the algae may be (*a*) one-celled, or colonies of similar cells, (*b*) filaments, branched or unbranched, or (*c*) large masses of tissue as in some sea weeds.

2. With few exceptions all are propagated vegetatively.

3. Asexual reproduction is accomplished by spores which may be motile or non-motile.

4. In all but the simpler forms, like those of Protococcus and the blue-green algae, sexual reproduction occurs. The gametes may be of the same size, or of very unequal size, motile or non-motile. In plants

like Vaucheria and Fucus the gametes are about as highly specialized as in the highest plants.

5. In the green algae, as a rule, the zygote passes into a state of dormancy, or resting stage, before germination. In the brown and red algae, on the contrary, the zygote does not pass into a resting stage but germinates soon after it is formed.

6. The zygote germinates into an individual like the parent (Spirogyra, Vaucheria, Fucus), or it may first produce swarm spores which in turn grow into plants like the parent plant (Oedogonium). The red algae (Rhodophyceae) constitute a notable exception. Here the zygote develops a number of filaments, collectively known as a spore fruit or cystocarp. These filaments (sporogenous filaments) form spores (carpospores) at their free, or distal extremities. In Batrachospermum and Lemanea the carpospores on germination give rise to a more simple filamentous juvenile form from which the adult parts of the plant arise as branches. In the Charales the zygote gives rise on germination to a filamentous juvenile form upon which the adult plant arises as a bud.

7. As a rule, the zygote is the diploid structure, the plant producing it being the haploid structure. The reduction in the number of chromosomes from 2x to x takes place as the zygote germinates. In Fucus and in similar brown algae the plant body is the diploid structure. The haploid structure is represented by the gametes alone. The reducing division takes place in the first division in the antheridium, and in the first division in the oögonium. In this respect Fucus resembles the higher vertebrate animals. In Dictyota and in many red sea-weeds, the haploid and diploid structures are distinct and separate individual plants, which in the vegetative state appear alike. The tetrasporic plant is diploid and the one bearing the sex organs is haploid.

TOPICS FOR REVIEW AND DISCUSSION

What pigments impart the characteristic color to Oscillatoria? How do these pigments differ in solubility?

What is a colony? An undifferentiated colony? A differentiated colony?

What algae do you know which form filamentous colonies?

What is a hormogonium?

Which blue-green algae mentioned in the text does not bear spores?

Of what economic importance are the blue green algae?

When troublesome in water supplies how are they gotten rid of?

Explain the progressive gliding movement of Oscillatoria and Navicula or Pinnularia.

How does the desmid Closterium turn a somersault?

Why have diatoms been referred to as "jewels of the plant world" and "grasses of the sea"?

What plants live in "glass houses"?

What is an auxospore?

What is diatomaceous earth?

Do all diatoms move or glide in the water?

Of what characteristic forms are the chloroplasts in the Zygophyceae?

Why are bacteria classed with the Schizophyta?

Do bacteria develop spores?

Name some bacteria which cause disease. Some that are useful to man.

What are some notable bacterial diseases of plants?

In what respect are bacteria sanitary agents?

What is crown gall?

Who was Erwin F. Smith? What important contribution to science did he make?

Why have the slime moulds (Myxomycetes) been regarded both as animals and as plants?

What vegetable crop is affected by a parasitic slime mould?

Using the life cycle diagrams given in the text as suggestions write life cycle diagrams of the following: Cocconeis, Rhopalodia, Pediastrum, Volvox, Cladophora, Fucus, Lemanea, and Polysiphonia. (Life cycle diagrams may be correctly written in a number of ways.)

Does a young colony of Pediastrum have as many cells as an adult colony of the same species?

In what respect is a Spirogyra filament a colony?

Who was Pringsheim? Of what modern botanical journal was he the founder?

What is the Brownian movement? Have you seen Brownian movement in any alga mentioned in the text?

What are isogametes? Heterogametes?

What are sporangia?

What are gametangia?

Is an oögonium a gametangium?

What is the difference between the oögonium and the egg?

What is a zygote as used in the text?

What process in plants created the diploid structure?

What is the diploid structure?

What is the haploid structure?

How is a diploid cell changed to a haploid cell?

What is meant by the dry land phase of an aquatic plant?

What algae do not reproduce by gametic union?

What is the basis for speaking of the egg of a plant like Fucus as female and of the sperm as male?

Would you apply the terms male and female to the gametes of Cladophora?

What is a holdfast?

What is the difference in function between a holdfast and a rhizoid?

Vaucheria may live upon earth. How does it secure water from the soil?

Is the ability of Vaucheria to heal wounds of any value to the plant?

Where do the largest algae grow?

What algae belonging to the Chlorophyceae are red in color?

What is meant by the expressions "red snow" and "red rain"?

What conspicuous algae may one find in bodies of fresh water throughout the winter?

Is Spirogyra injured by being frozen in ice?

Would fish live naturally in a body of water were there no algae in the water?

In what respect do polar bears owe their existence to microscopic plant life?

Are the red sea-weeds classed as Rhodophyceae because of their color?

Do all Rhodophyceae live in salt or brackish water?

What is meant by the juvenile form of an alga?

What is the significance of the brown and red color in sea weeds?

From what seaweeds may iodine and potash be derived?

What is agar? Give some uses of agar.

What is the eye-spot in algal cells? What is supposed to be its function?

Algal spores and gametes are sensitive to light. Is this sensitiveness of any value to the plants?

Algal filaments, such as Spirogyra are heavier than water. What enables them to form floating masses?

How do branches arise in filamentous algae?

What is a cystocarp?

How does the cystocarp of Polysiphonia differ from that of Batrachospermum?

Why are the asexual spores of Polysiphonia called tetraspores?

In what sea-weeds are motile cells wanting?

In what class of algae does the zygote germinate in the oögonium?

In what algae are the eggs eliminated from the oögonia before fecundation?

Which algae may grow deepest in the water? Why?

Which brown alga produces tetraspores?

What small alga grows on the shady side of tree trunks?

What algae do you know that are able to withstand wide extremes of heat, cold, and dryness? What do you think enables them to do so?

CHAPTER XV

THALLOPHYTA, FUNGI

The fungi include a large assemblage of plants representing more than forty thousand known species. They are of about the same structural rank as the algae, but differ from the latter in the *absence of chlorophyll.*

Fungi are, therefore, incapable of making their own food, which must be secured from other organic bodies. When they secure food from living organisms, fungi are termed *parasites;* if the source of food be dead organic matter, the fungus is known as a *saprophyte.* Many fungi are able to live both as parasite and saprophyte.

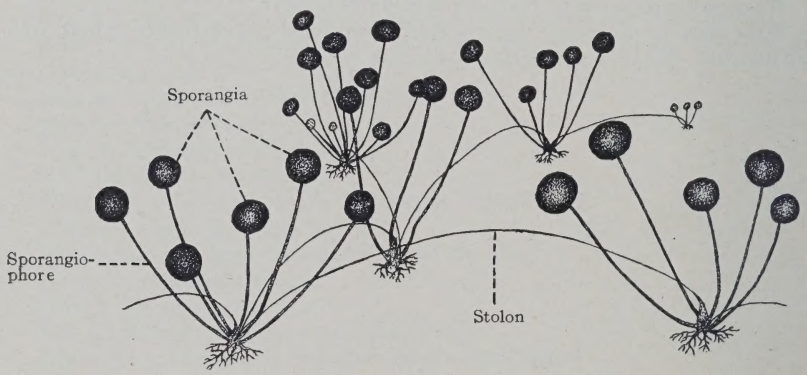


FIG. 248.—*Rhizopus nigricans.* Habit.

For convenience and simplicity we shall speak of the fungi as embracing two great sub-divisions: the Phycomycetes (algal-fungi), and the Mycomycetes (Eumycetes), or true fungi.

PHYCOMYCETES (ALGAL-FUNGI)

The Phycomycetes are called algal-fungi because of their resemblance in structure and reproduction to such algae as Vaucheria.

The mycelium, or plant body, consists generally of tubular, multinucleated filaments, which are without cross walls except where reproductive organs are formed; the mycelium of the Mycomycetes is septate. In some cases, however, the mycelium of the Phycomycetes may be septate.

Rhizopus.—As our first representative of the Phycomycetes we shall select a very common bread mould, *Rhizopus nigricans* (*Mucor stolonifer*), which will develop almost invariably upon bread kept in a moist, warm place, from spores that are in the air. If a piece of moist bread be exposed to the air for a few minutes, and kept in a warm place under a bell jar or other vessel, a crop of mould should develop in a day or two.

The Plant Body or Vegetative Mycelium.—The young plant of Rhizopus appears as a weft of fleecy white mycelium on the surface of the bread. Save in older plants and where reproductive bodies are formed, the mycelium consists of branched tubular filaments* (Fig. 249). With age the walls of the hyphae turn dark or smoky brown. In the bread is the nutrient mycelium which digests and absorbs the food. From certain places in this mycelium, aerial stolons are developed.

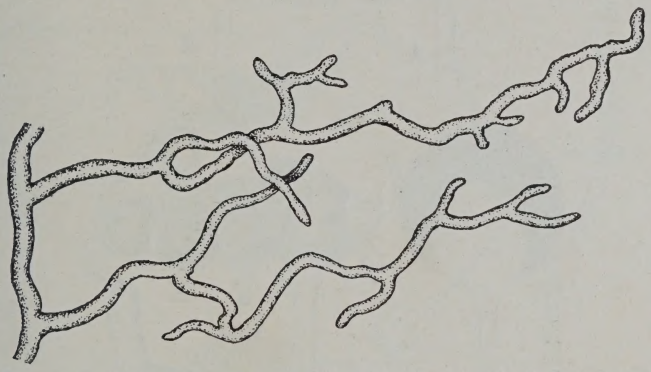


FIG. 249.—*Rhizopus nigricans.* Mycelium from inside the substratum.

The stolons spread readily and extensively over the bread or other substratum, sending into or toward the substratum rhizoid-like branches, and into the air clusters of *sporangiophores* (Fig. 248).

Asexual Reproduction.—Asexual reproduction is accomplished by spores borne in globular sporangia at the ends of stout upright hyphae, the sporangiophores (Fig. 250, A-C). When mature the wall of the sporangium is very brittle, and is readily broken.

The sporangium arises as follows: the upper end of the young sporangiophore enlarges into a globular head, into which flows dense cytoplasm and many nuclei. The head or sporangium is now separated by an arched cross wall, the columella (Fig. 250, A, B, C). The contents of the sporangium, by progressive cleavage (see page 26), give rise ultimately to numerous rounded spores with dark or smoky brown walls. Each spore contains one or more nuclei (Fig. 250, E, F).

* A single filament is called a *hypha;* plural, *hyphae.*

Sexual Reproduction.—Rhizopus nigricans is dioecious, so that unless mycelia of the two sexes grow intermingled, zygotes will not be formed. In laboratory cultures, if mycelia of different sexes be grown side by side upon the culture medium so that the hyphae of one will intermingle or interlace with those of the other, a windrow of zygotes will appear

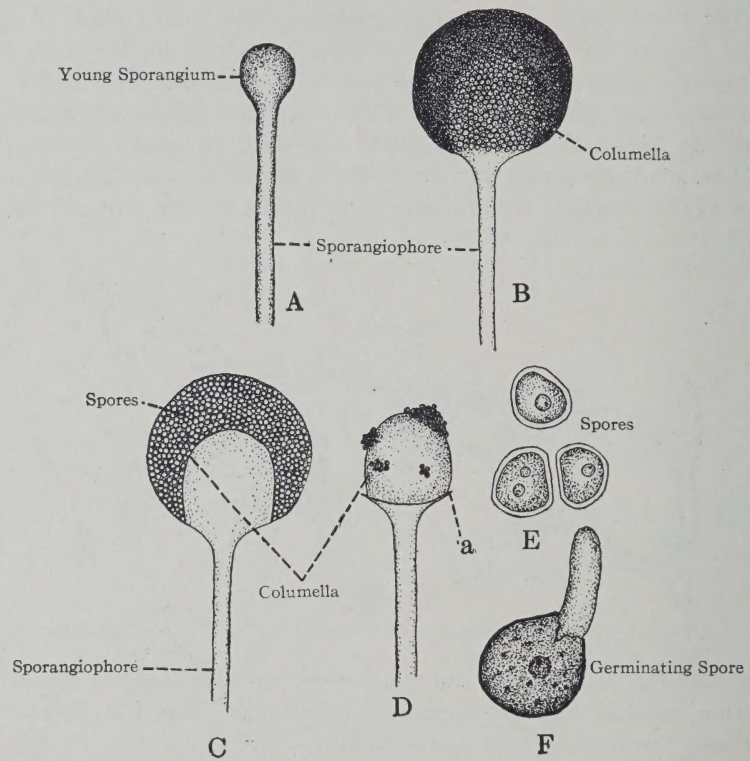


FIG. 250.—*Rhizopus nigricans.* The sporangium. A, a very young sporangium. B, sporangium almost mature. C, same as B, but in section, showing columella and spores. D, old columella with a few spores still attached; remains of sporangium wall, *a*. E, spores. F, germinating spore.

along the line at which the mycelia meet and intermingle. If bits from the strip or windrow be examined, all stages in the formation of the zygotes may be seen.

The process is briefly as follows: short, club-shaped branches from neighboring hyphae of opposite sex meet end to end (Fig. 251, A). These branches are progametangia. From the end of each of these a cell is cut off (B). These cells, which contain several nuclei, are the gametangia. The gametes within, which contain two or more nuclei, are sometimes

called *coenogametes*. An opening is now formed between the two gametes, and the contents unite, the nuclei fusing in pairs. This phenomenon is known as multiple fecundation, or multiple fusion of gamete nuclei. The zygote soon reaches maturity, developing a thick, complex cell wall which is black or dark brown, and very rough or warty externally (C, D).

Germination of the Zygote.—After a period of dormancy, and on the return of favorable conditions, the zygote germinates, sending out a short

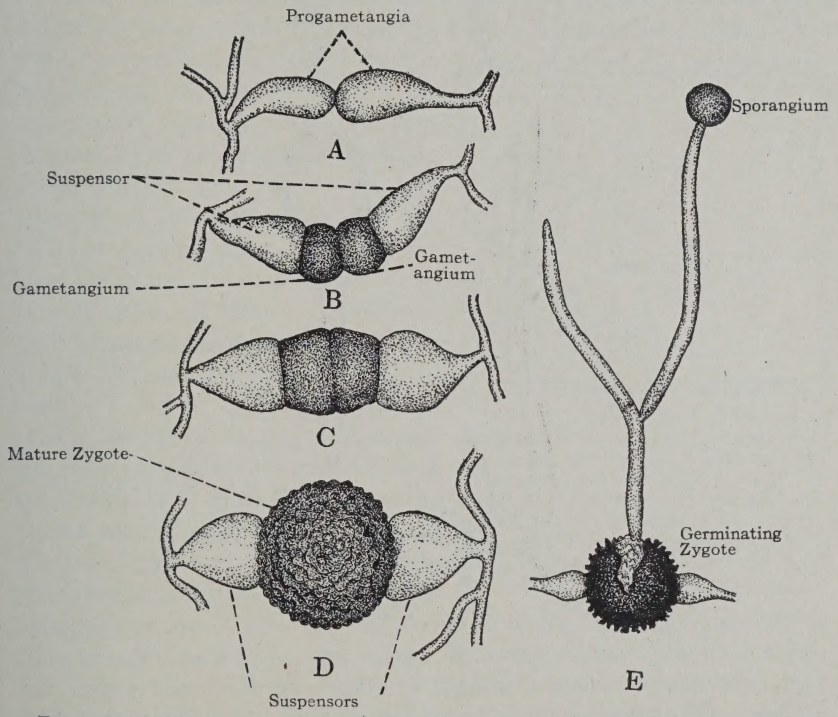


FIG. 251.—*Rhizopus nigricans*. Formation and germination of zygote. A–D, steps in conjugation, ending in the mature zygote. E, germination of zygote (Mucor), (E after Brefeld.)

hypha which develops a sporangium at its distal end (Fig. 251, E). The spores in this sporangium are the beginnings of new life cycles. Approximately one half of these spores are functionally of one sex, and one half of the opposite sex, the mycelium resulting from any one spore will, therefore, be functionally unisexual.

The Haploid and Diploid Structures.—The zygote and hypha resulting from its germination probably represent the diploid structure. If the reduction in the number of chromosomes takes place during or following

the germination of the zygote, the spores in the sporangium of Fig. 251, E, and the mycelia resulting therefrom will represent the haploid structure.

Monoecious and Dioecious Mycelia.—A monoecious mycelium bears two kinds of gametes, male and female. One mycelium represents, therefore, the complete haploid structure of a life-cycle. When the

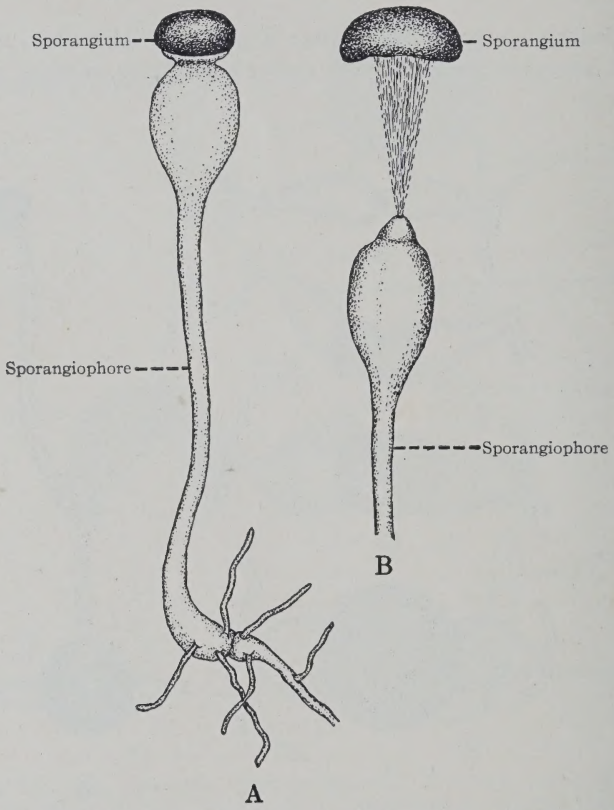


FIG. 252.—*Pilobolus crystallinus*. A, Sporangiophore. B, sporangium shot off from sporangiophore (the Pilobolus "gun" in action). (A after Brefeld; B after Zopf, from Schenck.)

mycelium is dioecious, one individual mycelium bears one kind of gamete, and another mycelium the other kind of gamete. Under such circumstances there are two haploid individuals in a life cycle.*

When a monoecious mycelium propagates asexually by spores, all of the spores are functionally bisexual, and all the resulting mycelia will be

* In recent literature the two mycelia are spoken of as + and −, the (+) mycelium representing the female, and the (−) representing the male. The (+) mycelium is usually more vigorous than the (−) mycelium. Dioecious species are now frequently referred to as *heterothallic*, while the monoecious forms are designated as *homothallic*.

monoecious. If a dioecious mycelium reproduces asexually by spores, the male mycelium will develop male spores, and male mycelia will always result. If the mycelium be female, only female mycelia will result from asexual reproduction.

Some species of moulds are monoecious. One mycelium constitutes the complete haploid structure in a life-cycle. The spores developed upon the hypha coming from the zygote, will all be of one kind, or bisexual, instead of two kinds as in the case of *Rhizopus nigricans*.

Pilobolus.—Belonging to the same group as Rhizopus is the interesting mould Pilobolus, which grows on the dung of herbivorous animals. The stout sporangiophore has a large, bulbous expansion just below the sporangium (Fig. 252, A). This enlargement is a kind of explosive apparatus, or pop gun, by which the sporangium is expelled into the air, and also a sense organ by which the sporangiophore responds to the direction of light. If plants of Pilobolus with maturing sporangia be placed in a dark chamber provided with a small window to admit light, it will be seen after a few hours that the window will be peppered over with the small, black sporangia, and that the sporangiophores will all be inclined toward the window (Fig. 253). The sporangiophore is positively phototropic, and the sensitive portion is in the bulbous swelling. It has been found that in some cases the sporangia have been thrown a distance of six feet in a horizontal direction. The sporangia adhere to the object against which they strike.

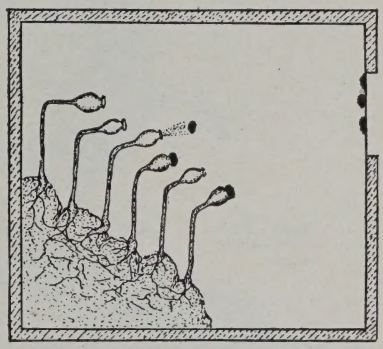


FIG. 253.—Pilobolus. Response of sporangiophore to light. A culture of the fungus is placed in a box, and light is admitted only through a small window. The sporangiophores bend toward the window, in response to the stimulus of light, and the sporangia are shot off forcibly against the window to which they adhere.

In nature Pilobolus grows on dung close to the ground. The sporangia are shot up into the air toward the light, striking blades and stems of grasses and other plants. The spores are said to grow readily only after having passed through the alimentary tract of herbivorous animals. The sporangia adhering to forage plants are eaten by the animals. The explosive discharge of the sporangia is, consequently, an ecological adaptation in the life of Pilobolus.

Albugo.—As a second representative of the Phycomycetes we shall select for more detailed presentation the parasite, *Albugo candida*, found in the spring on the Shepherd's Purse plant (*Capsella bursa-pastoris*), and producing what earlier investigators called the "White Rust."

Vegetative Structure.—The plant body of Albugo consists of a system of tubular, branched, multinucleate filaments, which live within the intercellular spaces of the host plant. It is, consequently, an internal parasite. The manner in which it secures nourishment from the host cells will be explained in a later paragraph.

The presence of the parasite is recognized in its earlier stages as white pustules, or blisters, varying in size from that of a pin head to large white expansions covering longer stretches of the stem or leaves (Fig. 254, A).

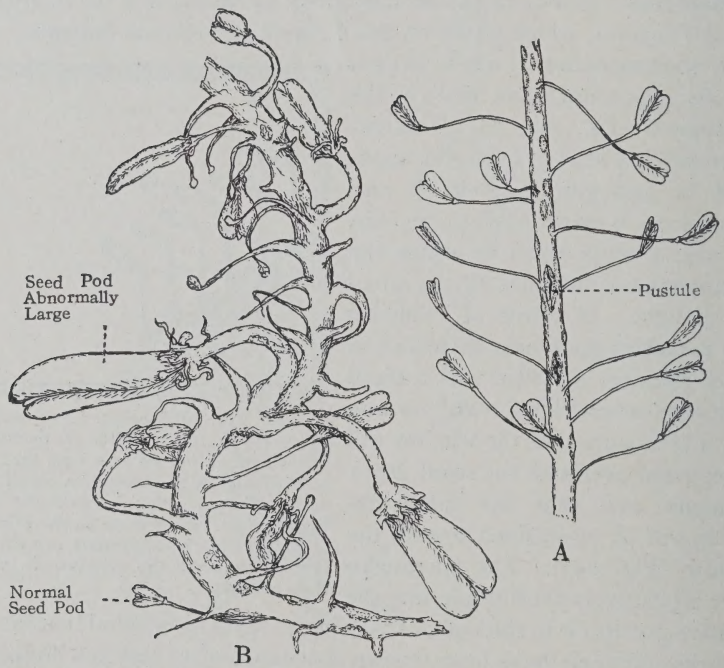


FIG. 254.—Stems of Shepherd's Purse affected with the White Rust (*Albugo candida*). A, stem of normal size, showing pustules of sporangia. B, portion of stem, showing a later stage of the disease. The parasite causes the stem and seed pods to become greatly enlarged and distorted (hypertrophy). These enlarged diseased stems contain enormous numbers of zygotes of the fungus.

These pustules are caused by numerous colorless *sporangia* developed in immense numbers just beneath the epidermis of the host. The *sporangia* were formerly called *conidia.*

Asexual Reproduction.—A cross section of the stem or leaf of the host, passing through a pustule, will illustrate the manner in which the sporangia are developed and how the pustule is formed (Fig. 255, A, B). In a pustule still covered by the epidermis the sporangia will be seen in rows. Each row may be traced back to an upright, club-shaped hypha,

the *sporangiophore* (Fig. 256). From the upper end of the sporangiophore the sporangia are abjointed singly, producing the row, the outermost one, next to the epidermis, being the oldest. The sporangia are connected by narrow necks formed from the cell wall (Fig. 257, A). The accumulation

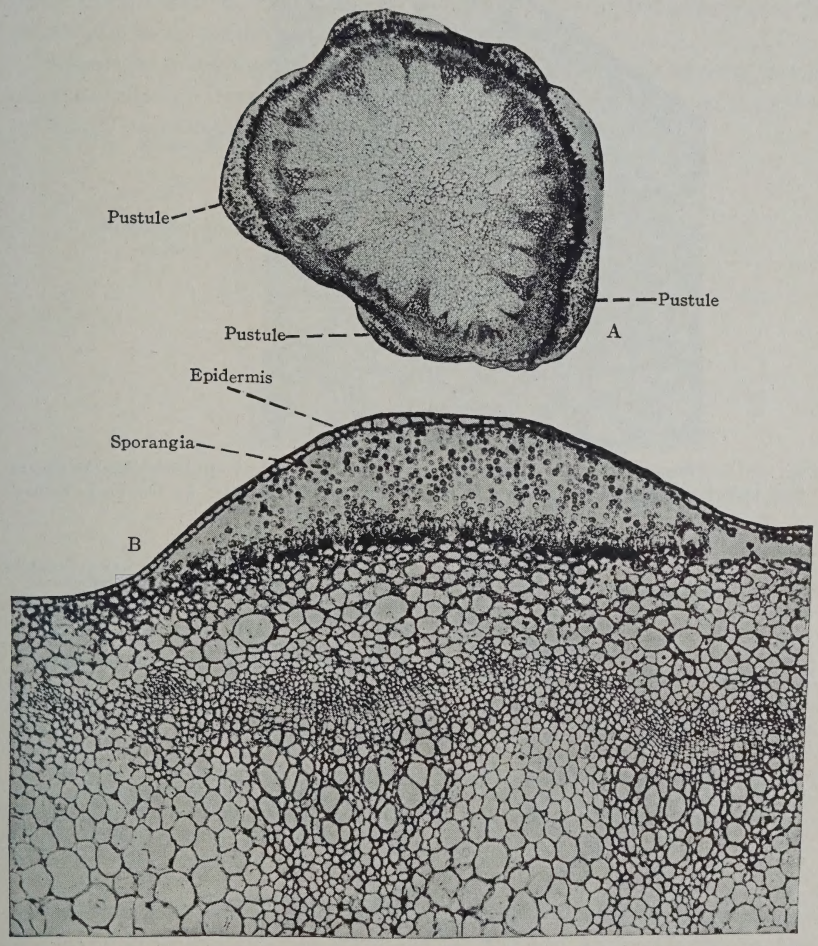


FIG. 255.—*Albugo candida.* A, cross section of infected stem of Capsella, showing blisters filled with sporangia. B, portion of section showing pustule more highly magnified. (Photo. by Dr. E. J. Kohl.)

of sporangia gradually pushes out the epidermis until it is finally ruptured and the sporangia are set free. The masses of sporangia appear to the naked eye as white flour. They are scattered by the wind.

Germination of Sporangia and Infection of the Host.—Under favorable conditions of moisture and temperature the sporangia will germinate. Each

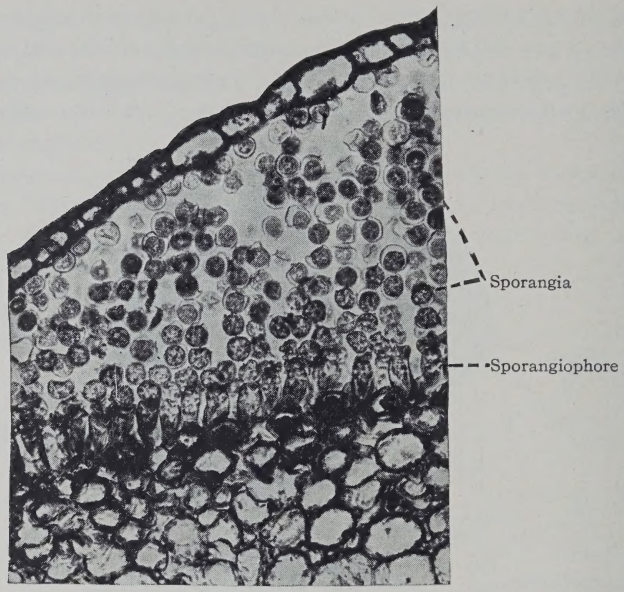


FIG. 256.—*Albugo candida*. Portion of pustule still covered by epidermis highly magnified, showing sporangiophores and chains of sporangia. (Photo. by Dr. E. J. Kohl.)

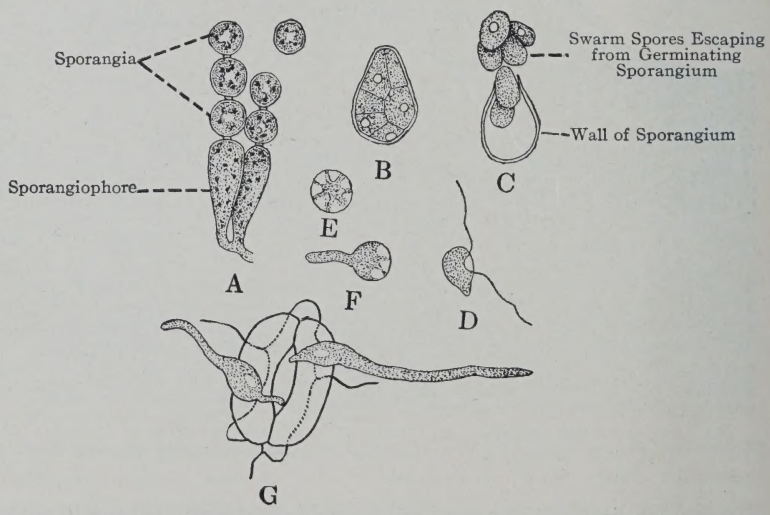


FIG. 257.—*Albugo candida*. Asexual reproduction. A, two sporangiophores, each forming a chain of multinucleated sporangia. B, a sporangium which has produced within itself as many swarm spores as it had nuclei. C, swarm spores escaping from sporangium. D, a swarm spore. E, a swarm spore which has come to rest and has lost its cilia. F, G, swarm spores germinating and infection tubes entering stoma of the host. (B–G, from DeBary.)

contains several nuclei. The contents divide into several cells, which escape as biciliate swarm spores (Fig. 257, B, C, D). If the germination occurs on a suitable part of a host, as a young, tender portion, infection will take place. The swarm spores come to rest and germinate by sending out a germ tube (F, G). This germ tube penetrates the tissue, and the parasite is soon established within its host.

From the foregoing it is readily seen that the sporangia are the means of rapid infection, the mycelium in one diseased host plant being sufficient to supply sporangia to infect many other near-by plants.

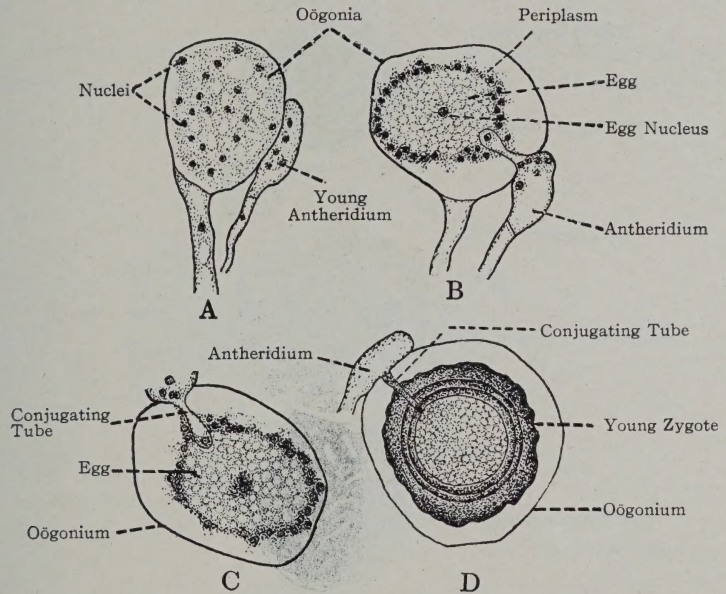


FIG. 258.—*Albugo candida.* Sexual reproduction. A, young oögonium and antheridium. B, same after separation of egg from periplasm. C, section of oögonium, showing antheridial tube after its penetration of the egg. D, nearly mature zygote inside old oögonium, the antheridial tube still extending into the thick wall of the zygote. (C, from Wager, according to Mottier.)

Sexual Reproduction.—After a time sporangia will cease to be developed on a given host, and some of its stems, leaves, and seed pods will appear of an abnormal size; i.e., over developed (hypertrophy) and of a dark or brownish color. If the stem of such plants be examined, numerous, yellowish or brown zygotes will be found distributed throughout its tissues (Fig. 259, A). Each zygote has a thick, brown wall of two or more layers, with irregular thickenings on the outside.

Oögonia and Antheridia.—The zygote is developed, of course, from the fecundated egg. The oögonia and antheridia arise from separate

hyphae deeply seated within the host. The former is at first a globular cell with dense cytoplasm and many nuclei. Near it grows the antheridium, an irregular, club-shaped cell, containing several nuclei (Fig. 258, A). Within the oögonium all the nuclei but one, which remains in the center, pass into a zone along the periphery of the cell. Within this zone of nuclei a plasma membrane is formed delimiting a large, globular egg with its nucleus (Fig. 258, B, C). The cytoplasm and nuclei between the egg and the wall of the oögonium is the *periplasm.*

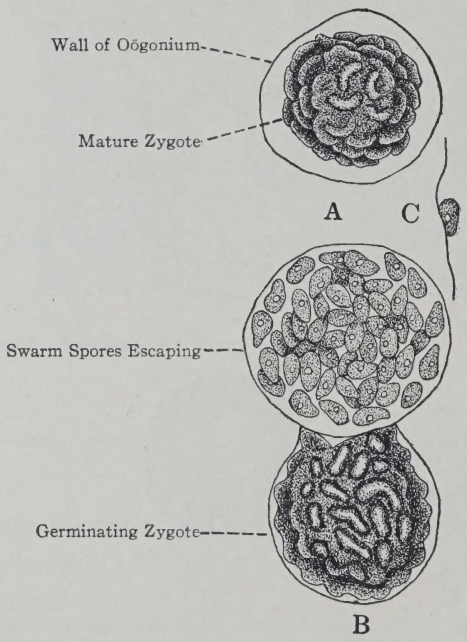


FIG. 259.—*Albugo candida.* A, surface view of mature zygote still enclosed in wall of oögonium. B, swarm spores escaping from germinating zygote. C, one swarm spore. (B, C, from DeBary.)

As the egg is being differentiated, the antheridium sends a tube into the oögonium, through the periplasm into the egg. The end of the tube opens, and one nucleus of the antheridium enters and fuses with the nucleus of the egg. This constitutes fecundation. The zygote develops its thick wall and passes into a dormant state (Fig. 259, A). The thick wall, or at least a part of it, is doubtless formed at the expense of the periplasm.

In some species, as in *Albugo bliti,* the egg contains several nuclei, but not all are functional.

Germination of the Zygote and Infection of the Seedling Host.—In our climate the zygote passes the winter on the ground within the dead

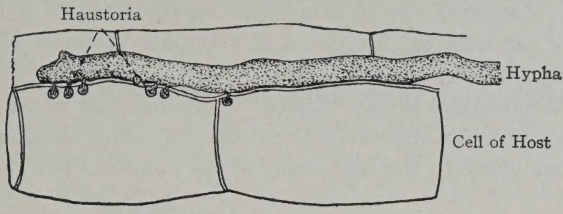


FIG. 260.—*Albugo candida.* Hypha between pith cells of the host plant. (From DeBary.)

stems of the host plant. In the spring when the seeds of Capsella germinate the zygotes also germinate. The germination of the zygote results

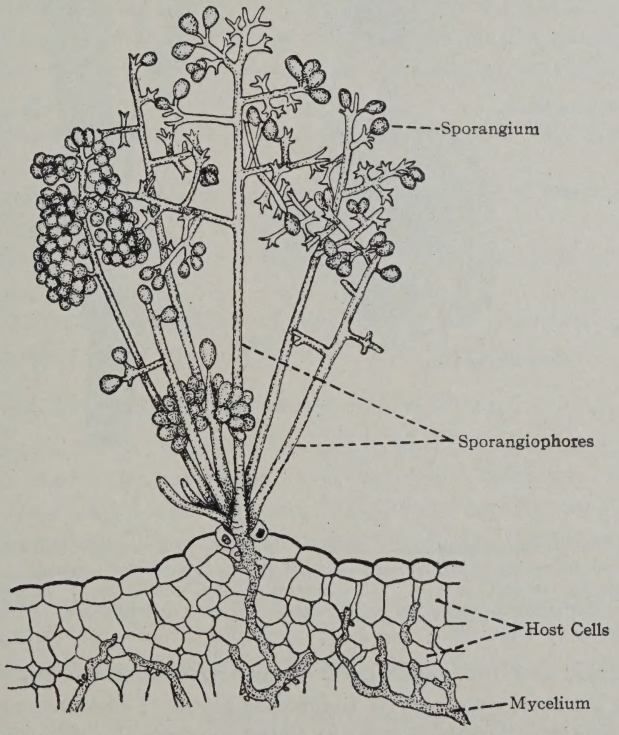


FIG. 261.—Section of leaf with much branched sporangiophores of *Plasmopora viticola* emerging through a stoma. (Adapted from Millardet's figure in Naturlichen Pflanzenfamilien.)

in the formation of many swarm spores (Fig. 259, B). If the swarm spores happen to come in contact with any part of the seedling host, infection will take place, and the seedling will grow up with its parasite.

How Albugo Secures Food from Its Host.—As shown in Fig. 260, the hyphae send into the cells of the host numerous very minute branches, *haustoria*, or suckers, the ends of which enlarge as soon as the cell wall is penetrated, so that each appears as a minute globular body connected with the hypha by a slender neck.

Other Destructive White "Rusts."—Among other parasites resembling Albugo in character and life history are the downy mildew of the grape (*Plasmopara viticola*), the late blight of the potato (*Phytophthora infestans*

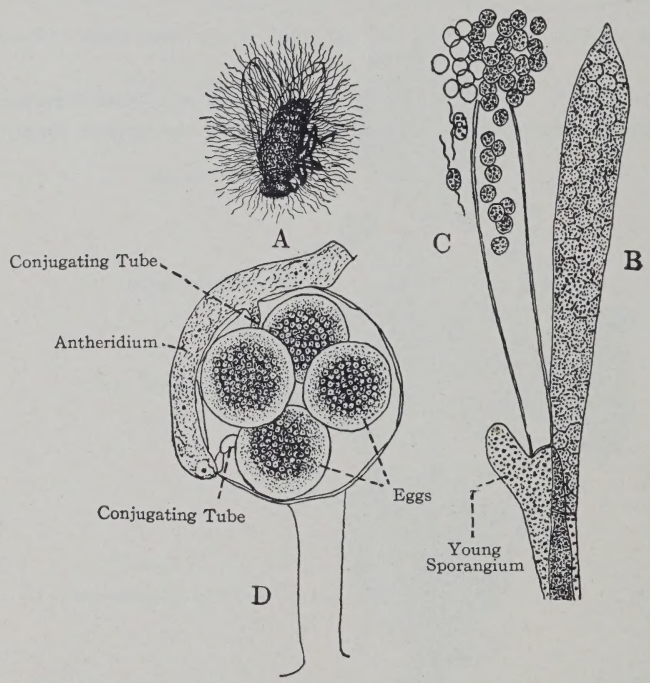


FIG. 262.—Reproduction in Achlya. A, body of a common fly with radiating filaments of the mould. B, sporangium with swarm spores nearly mature. C, sporangium discharging swarm spores. D, oögonium with antheridium closely applied, and antheridial tubes penetrating to the eggs. (B and C, from Engler & Prantl; D, from Trow.)

DeBary), and the damping-off fungus (*Pythium debaryanum*), the last being often very destructive to seedling plants. The sporangia of Plasmopara and Phytophthora are not found beneath the epidermis of the host as in Albugo, but on the outside. The sporangiophores, which may be branched, grow out through the stomata or break through the epidermis (Fig. 261).

Water Moulds.—The mycelium of the water moulds is similar in structure to that of Albugo. These fungi may live as parasites but they

are usually saprophytes. They develop on the bodies of fishes and batrachians, and their eggs, or on the bodies of insects and other small animals that have fallen into the water. Their nature and reproduction are illustrated in Fig. 262.

The Fly Mould.—Species of the genus Empusa attack living insects. *Empusa muscae* is a parasite of the common house fly. The diseased flies are sometimes found in the autumn adhering to window panes and surrounded by a whitish halo of conidia, which have been shot off from the conidiophores protruding from the insect's body. The life history of this fungus is similar to that of the water moulds.

Classification of the Phycomycetes

The Phycomycetes may be included in the following orders:

1. *Chytridiales.*—These are among the simplest of the group, some consisting of a single small cell. Many are parasites on other fungi or on algae. Some species of Synchytrium are parasitic on seed-bearing plants.

2. *Saprolegniales.*—This order includes the water moulds, Saprolegnia, Achlya, etc.

3. *Peronosporales.*—This large group includes Albugo, Plasmopara, Peronospora, Pythium, and Phytophthora.

4. *Mucorales.*—These are the bread moulds or pin moulds of the genera Rhizopus, Mucor, etc.

5. *Entomophthorales.*—Members of this order are parasitic upon insects, such as species of Empusa mentioned in the foregoing.

MYCOMYCETES (EUMYCETES)—TRUE FUNGI

The vast majority of fungi belong to the Mycomycetes, or true fungi. Their mycelium, as a rule, consists of septate hyphae. With few exceptions they may be grouped into two great subdivisions, namely, the Ascomycetes (sac-fungi) and the Basidiomycetes* (basidia fungi) among which are included smuts, rusts, mushrooms, and puffballs.

A typical sac, or ascus, is an elongated cell bearing commonly eight spores, although the number of spores in the ascus may vary (Fig. 274). A typical basidium is an elongated, or club-shaped cell bearing from one

* Another group known as *Fungi Imperfecti*, which produce conidia only, is of very great economic importance. Many of these fungi prove, upon investigation, to be stages of the groups already mentioned, particularly of the Ascomycetes. Many of the *Leaf Spots* and *Fruit Rots* belong here.

Still another group known as *Mycelia Sterilia* produce no spores at all, existing only in the form of mycelia. Their hyphae live in the soil attacking the underground parts of plants.

to four spores on very short and slender stalks at the upper end of the cell (Fig. 283).

ASCOMYCETES

Cultivated or Common Yeast (*Saccharomyces cerevisiae*).—In the classification of the fungi, yeasts are sometimes included in the Ascomycetes, being placed in the sub-class Hemiascineae, because of the fact that when spores are formed the cell bearing them resembles a sac or ascus common to the Ascomycetes.

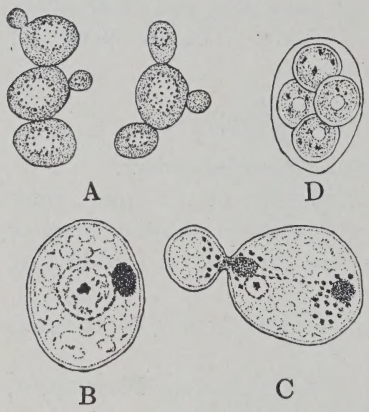


FIG. 263.—Yeast (*Saccharomyces cerevisiae*). A, actively growing cells showing budding. B, stained cell showing nucleus, cytoplasm, vacuole, and one conspicuous granule in vacuole. C, stained cell showing budding, the nucleus of the parent cell having divided. D, cell containing four spores. (A, D, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers. B, C, from Wager; D, from Riess.)

The yeast plant is unicellular, the cells often adhering to form a chain-like colony of cells. Rarely do the colonies become sufficiently long to be considered hyphae (Fig. 263, A). The cell contains one nucleus, and usually a large central vacuole and food granules (B).

Vegetative Propagation.—The cells multiply by a process of cell division termed "budding." A small bead-like protuberance is sent out at the end or side of the cell. The nucleus divides, and one of the daughter nuclei passes into the bud (Fig. 263, C). As the bud increases in size it is cut off by the completion of division. The new cell may soon divide in the same manner, and at the same time the parent cell may produce one or more buds at the sides or at the other end. If the new cells thus formed remain attached, a colony results.

Spore Formation.—Under certain conditions, as when the cells are cultivated on a piece of carrot or potato, internal cell division takes place, and two to four spores are produced (D). In this condition the yeast cell resembles a simple ascus.

Alcoholic Fermentation.—Yeasts are important in the economy of man chiefly because of certain useful by-products resulting from their life activity. The more important of these products are alcohol and carbon dioxide. When yeast uses glucose as a food, these two compounds result according to the following chemical expression: $C_6H_{12}O_6 = 2C_2H_5OH + 2CO_2$.

Glucose, acted upon by zymase yields ethyl alcohol and carbon dioxide. In bread making the carbon dioxide liberated in the fermenting dough makes it rise.

The different species of yeast behave differently in regard to the fermenting substance, and this is an important matter in their use and classification. Some kinds of yeast consist of very small cells resembling bacteria, but they are distinguished from bacteria by the fact that yeast cells divide by budding, while bacteria divide by fission. A fungal spore, which closely resembles a bacterium or a yeast cell, is distinguished from these two by sending out normally a germ tube on germination.

Sexual reproduction has been reported in Schizosacchromyces and in some other genera. Two cells unite and an ascus with eight spores is formed.

The Powdery Mildew.—Any common mildew, such as Sphaerotheca on the dandelion, Uncinula on the willow or Microsphaera on the lilac, will serve to illustrate the life history of one of the simpler Ascomycetes.

FIG. 264.—*Uncinula salicis*. Leaves of black willow, showing whitish patches of mycelium of the mildew, in which the small black perithecia, appearing as black specks, can be seen.

These mildews are external parasites. Their mycelium, which consists of septate hyphae, forms a whitish or cobwebby weft on the surface of leaves (Fig. 264). Nourishment is secured from the host by means of haustoria sent into the epidermal cells of the leaf (Fig. 265). In Phyllactinia special short hyphae penetrate through the stomata more deeply into the tissues, sending haustoria into the underlying parenchyma cells.

Asexual Reproduction.—Asexual reproduction is effected by means of *conidiospores*, or *conidia*. They are formed in single rows, abjointed from the ends of upright hyphae (conidiophores), which arise at right angles from the mycelium (Fig. 265). When conidia are numerous the mildew presents the appearance of frosty or powdery patches on the surface of the leaf. Because of this fact they are called "powdery mildews." The conidia are borne chiefly by the wind to new host plants, where they germinate and give rise to new mycelia.

Sexual Reproduction.—Later in the season the production of conidia ceases, and the mycelium develops the spore fruits (*perithecia*) as a result of sexual reproduction. The spore fruits are developed as follows: from adjacent hyphae two very short branches are sent up side by side, one being the oögonium and the other producing the antheridium (Fig. 266, A). The antheridium and its stalk are closely applied to the oögonium. An opening is formed between the two, and a nucleus from the antheridium

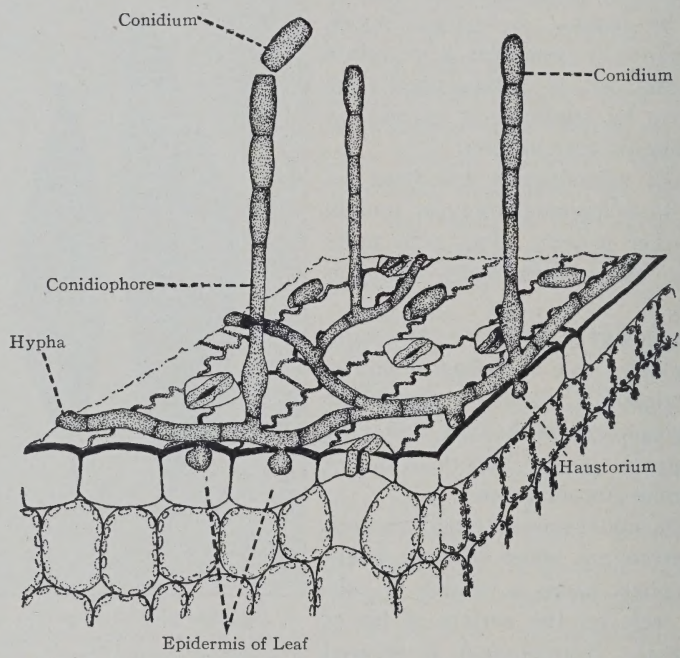


FIG. 265.—*Erysiphe graminis.* Formation of conidia in the mildew. Portion of a leaf of a grass, partly in section, showing mycelium, conidiophores, conidia and haustoria. Leaf tissue diagrammatic.

enters the oögonium and fuses with its nucleus (B). After fecundation the vegetative cover begins to grow up about the developing zygote enclosing it completely (C, D). This cover is derived chiefly from the hyphae that bore the sex organs. In the meantime the zygote produces a short row of cells. One of the cells near the end of this row, and which contains two nuclei that later fuse, develops into the single ascus in Sphaerotheca (D, *a*). The ascus contains two to eight ascospores. In Microsphaera and some other mildews two or more asci grow out of the binucleate cell. In some mildews the perithecia are without external appendages, but in others, as the spore fruit matures, characteristic

appendages are developed from the superficial cells of the perithecium (E, F).

The spore fruit with the contained ascospores serves to carry the mildew through the winter.

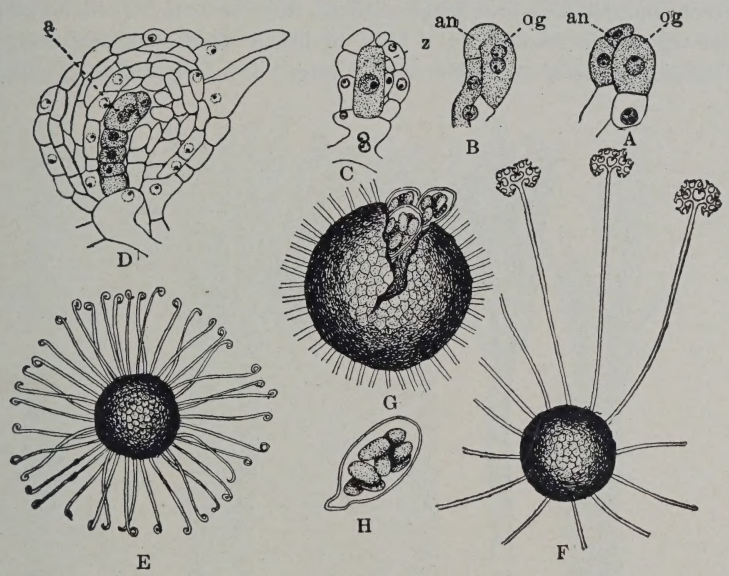


FIG. 266.—Sexual reproduction and formation of the perithecium in the mildew. A–D, first steps in the process in Sphaerotheca. A, antheridium (*an*) and oögonium (*og*) on portions of adjacent hyphae. B, union of oögonium and antheridium, with the gamete nuclei side by side. C, zygote (*z*) with the vegetative cover beginning to develop. D, row of cells (shaded) which have developed from the zygote. The large, binucleate cell (*a*) will give rise to the ascus. The wall of the fruit is almost complete. E, mature perithecium of Uncinula. F, perithecium of Microsphaera. G, perithecium of Uncinula, broken open and showing the escaping asci. H, one ascus of Uncinula. (A–D, from Harper.)

Diploid and Haploid Structures.—Those parts developing from the oögonium after fecundation, and producing the ascus or asci, constitute the diploid structure, inasmuch as the nuclei in those cells are descended from the zygote nucleus. The haploid structure is represented by the mycelium that bears the sex organs, and all subsequent parts of this mycelium resulting from purely vegetative growth. The shell or covering of the perithecium is, therefore, a part of the haploid structure.

Blue and Black Moulds.—Among simpler Ascomycetes that live saprophytically, as well as parasitically, are the genera Penicillium and Aspergillus. When mature the densely massed conidiospores appear blue-green or black, hence the source of their common names.

In sexual reproduction spore fruits are developed much in the same manner as in the powdery mildews, although the perithecia in some genera are much more complex than those of the mildews.

Asexual reproduction is accomplished by conidia, and the genera are usually recognized by the character of the condiophores. In Penicillium the erect conidiophore produces branches, each branch bearing a chain of spores, the whole resembling a kind of brush or broom (Fig. 267, A). The conidiophore of Aspergillus is enlarged into a globular swelling at

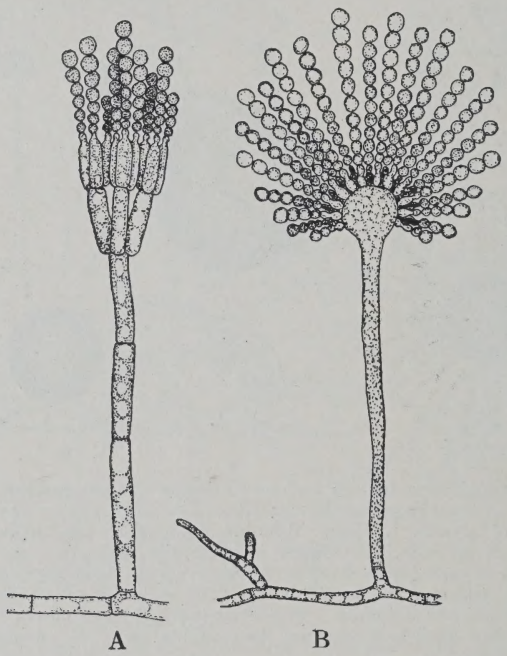


FIG. 267.—Conidophores of blue and black moulds. A, Penicillium. B, Aspergillus. (From Kny's chart.)

its upper end, from which grow out radially numerous short branches (Sterigmata), each producing a chain of conidia (Fig. 267, B). In the genus Sterigmatocystis each branch from the globular enlargement is further branched.

Black Knot and Ergot.—Two very well known parasitic Ascomycetes are the Black Knot (Plowrightia) of the plum and other fruit trees, and the Ergot (*Claviceps purpurea*) on rye and other grasses. Plowrightia attacks the twigs of the plum tree inducing the large, rough malformations known as Black Knot (Fig. 268). Claviceps produces the large, purplish or black, horny ergot grains, which appear instead of normal seeds in the head of rye and other grasses (Fig. 269).

The mycelium of the ergot is recognized in the tissues of the flowers of the rye plant. The fungus develops rapidly, and soon destroys the ovulary, replacing the normal kernel with the large mass of fungal filaments. This mass constitutes a "grain of ergot," and it is termed botanically a *sclerotium*, meaning here a hard, dry, horny mass of fungal tissue.

The sclerotium drops to the ground, where it passes the winter. The following spring it resumes growth and sends out from one to several cylindrical or cord-like masses of fungal tissue, pinkish or purplish in

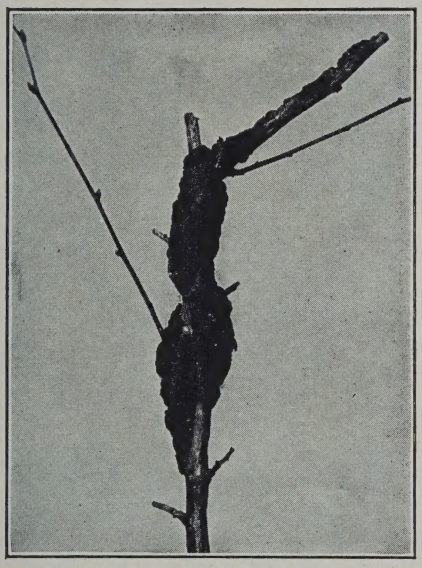


FIG. 268.—Twig of plum tree infected with the Black Knot fungus, Plowrightia. The black abnormal growth is the hypertrophied host tissue, in which are contained the mycelium and spores of the fungus.

FIG. 269.—Head of rye with mature sclerotia of ergot. (From Strasburger.)

color, and composed of bundles of numerous hyphae united laterally to form a pseudo-parenchyma (Fig. 270, A, *a*). Each cylindrical cord or mass bears at its free end a rose-colored head, in which numerous flask-shaped cavities, *perithecia*, are borne (B, C). The perithecia contain many slender asci, each with eight filiform ascospores (D). These ascospores when set free are borne to the young flowers of rye where infection takes place.

Development of Conidia.—Upon the diseased flower and before the sclerotium is developed, the mycelium produces conidia (Fig. 270, E). At the same time a sweetish fluid, known as "honey dew," is exuded.

This is sought by insects and, with the spores imbedded in it, borne to other host plants.*

Cordyceps.—Certain species of Cordyceps, which are related to ergot, are parasitic upon insects and fungi, one growing on the larvae of the May beetle (Fig. 271).

FIG. 270.—Ergot (*Claviceps purpurea*). A, sclerotium which has developed the bundles of hyphae ending in the rose-colored heads (*a*). B, longitudinal section of a head, showing location of perithecia. C, one perithecium enlarged; *as*, asci. D, ascus containing spores (*a*); with spores escaping (*b*); a single spore (*c*). E, hypha bearing conidia. (A–C, from Tulasne; D, E, from Brefeld.)

Cup-fungi.—The cup- or disc-fungi, which are included in the class Discomycetes, are among the larger and more commonly known fleshy Ascomycetes. They grow generally on decaying wood or on humus.

* From ergot is prepared for officinal use, under legal regulations, a powerful drug. The sclerotium is poisonous to stock if eaten in sufficient quantity, causing a malady which leads to the loss of hoofs, horns, hair, and tail.

The spore fruit, known here as an *apothecium*, is in the form of a fleshy cup or flattened disc, varying from dull to white or brilliant colors, and in size from that of a pin head or smaller, as in Ascobolus, to several centimeters, as in Peziza and Bulgaria, etc. (Figs. 272, 273).

Peziza, Bulgaria.—As mentioned above, the spore fruit, or apothecium, of Peziza is in the form of a cup or flat, circular disk. The vegetative mycelium, which lives in the substratum, consists of a weft of hyphae or cord-like mycelial strands. The spore-fruit is produced on the surface of the substratum. The inner surface of the cup, or upper surface of the disk, consists of a layer of club-shaped asci interspersed with numerous slender hyphae, often rich in oil, which are called *paraphyses*. The layer of asci and paraphyses constitutes the *hymenium*. One of the functions of the paraphyses is to supply food material for the developing asci (Fig. 274).

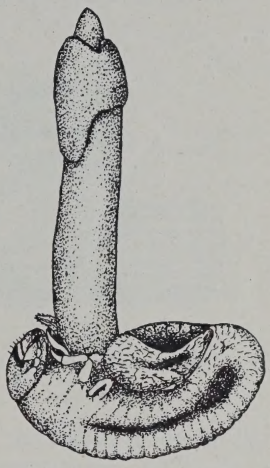


FIG. 271.—*Cordyceps herculea*. Young spore-bearing structure growing from larva of the May Beetle.

Sexual Reproduction, and the Formation of the Apothecium.—As in many other Ascomycetes, the spore-fruit consists of a reproductive part surrounded by a vegetative cover. Its development has been followed in

FIG. 272.—Urnula craterium. Apothecia in different stages of development, on dead branch of oak.

greatest detail in *Pyronema confluens*, a fungus whose yellowish or reddish apothecium is about one millimeter in diameter.

Several oögonia and antheridia take part in the formation of the apothecium. They arise on a weft of the mycelium side by side in a cluster (Fig. 275, A). The oögonium (*o*) is a large, globular cell, from the

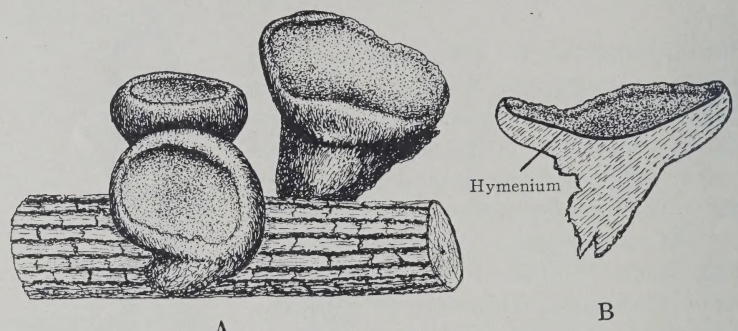


FIG. 273.—*Bulgaria inquinans*. A, apothecia in natural habitat on dead branch of elm. B, vertical section of apothecium.

top of which grows out a curved tubular cell, the trichogyne (*t*), which finally fuses with the upper end of the club-shaped antheridium (*a*).

FIG. 274.—*Bulgaria inquinans*. Vertical section of a part of the hymenium, showing asci and paraphyses.

The oögonium, antheridium, and trichogyne are multinucleate. The egg does not round up and separate from the wall of the oögonium. Its behavior in this respect resembles that of the Red Algae. The nuclei in the trichogyne disorganize; the wall between the oögonium and the trichogyne is dissolved, and some of the contents of the antheridium passes through the trichogyne into the oögonium, where the male and female nuclei fuse in pairs (B, C, D).*

From the surface of the oögonium will now grow out numerous branched *ascogenous* filaments (E). From the ends of these the asci will ultimately be formed as the result of a complex process of nuclear and cell division. During the development of the ascogenous hyphae there grow up among them many vegetative hyphae, which produce the paraphyses. At the same time the vegetative part of the plant increases and grows up about the asci and paraphyses, completely enclosing them. It will thus be seen that in the immature apothecium the hymenium is enclosed. As it matures, however, an opening forms in the top, and the hymenium is exposed. The apothecium may remain

* The accuracy of this statement has been questioned by some observers.

a deep cup, or growth may continue in such a way as to open out the cup into a flat disk.

From the foregoing we see that the development of the apothecium in the Discomycetes is similar to that of the perithecium in the mildews.

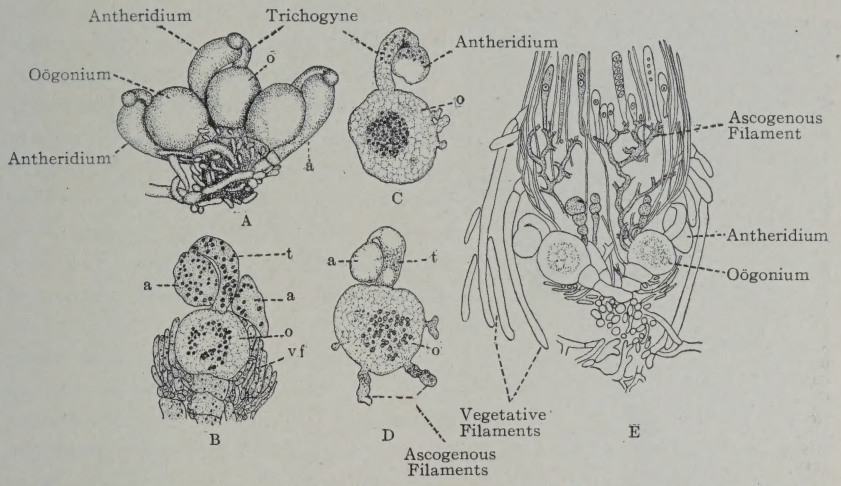


FIG. 275.—*Pyronema confluens*. Fecundation and early stages in the formation of the apothecium. A, cluster of oögonia (*o*), and antheridia (*a*). B, fusion of antheridium with tip of trichogyne; *vf*, vegetative filaments. C, fusion of male and female nuclei in pairs after dissolution of basal wall of the trichogyne. D, oögonium cut off from trichogyne by a new wall, and ascogenous filaments beginning to grow out from the oögonium. E, portion of a vertical section through a very young apothecium; ascogneous filaments bearing asci. (From Harper.)

Morchella esculenta.—The morel, which is often highly prized as a delicacy of the table, is one of the largest and most highly differentiated of the Discomycetes (Fig. 276). The irregular depressions in the crinkly head of the morel are lined with a hymenium bearing many asci. This part of the plant is regarded by some as a sort of compound apothecium. The morphological history of the morel is not well known. The vegetative mycelium lives in the soil.

The Truffle.—The truffle of commerce is the large spore fruit of certain species of the genus Tuber. These develop underground, where the mycelium lives saprophytically. The edible truffles are obtained chiefly from France and Italy. The species found in Indiana have small spore fruits which are said to be poisonous.

Lichens.—Lichens are very peculiar organisms, consisting of an alga and a fungus living together in such a way as to constitute a single plant. The fungus, generally an ascomycete, completely surrounds the algal cells (Fig. 277, C). In a sense the lichen is a fungus with algal cells imprisoned. The algal constituent is some unicellular plant like Proto-

coccus or some blue-green alga. The relation of the alga and fungus is a form of symbiosis known as *helotism*, a condition of enforced slavery on the part of the alga. The fungus obtains food from the algal cells, destroying some of them but not all. The algal cells seem to thrive and multiply as well as when existing alone in the normal state. Since the fungus concerned is usually an Ascomycete, lichens are sometimes regarded as members of the Ascomycetes which imprison algae in their thalli. In a small group of tropical lichens (*Cora pavonia* and other species) the fungal constituent is a Basidiomycete. The alga is usually some species of the Cyanophyceae or of the Protococcales.

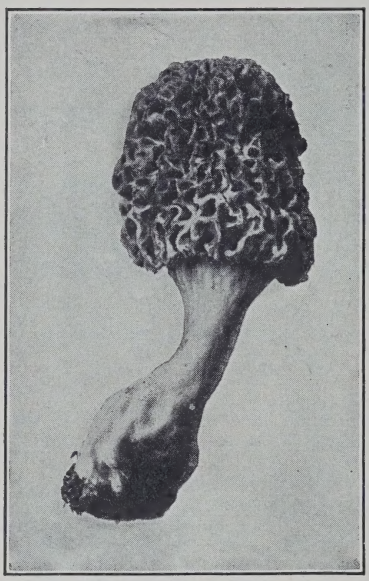


FIG. 276.—The mature sporophore of *Morchella esculenta*.

The grayish-green or bluish-green color of a lichen is usually dull in appearance because of the translucent fungal or gelatinous covering over the algal constituent. Many lichens have additional pigments such as yellow, orange, reddish, or brownish.

Based upon the form of the plant body, three classes of lichens are recognized: (1) *Crustaceous* lichens, with poorly defined mycelium, which frequently penetrates the substratum and forms incrustations on rocks, etc. (Fig. 278, B); (2) *Foliaceous* lichens, flat and leaf-like, with lobed or irregular margins (Parmelia, Physcia, Figs. 277, 278, A); and (3) *Fruticose* lichens, gelatinous (Collema), bushy and erect (Cladonia, Fig. 279), or pendent (Usnea, Fig. 280). Some, however, are filamentous.

The Thallus.—In gelatinous lichens, such as Collema, in which the alga is a species of Nostoc, the filaments of both alga and fungus are irregularly distributed in a gelatinous matrix (Fig. 281, A).

The structure of the forms more commonly encountered may be illustrated by Parmelia or Physcia. The plant body of Parmelia is a flat, irregularly lobed, tough, leathery, grayish-green thallus. The lower side is generally whitish. The thallus is fastened to the substratum by numerous *rhizines*, which are strands of mycelium. The upper and lower portions of the thallus form a firm, tough cortex composed of interwoven fungal filaments. Inside the cortex, but nearer the upper surface, is a region of looser fungal tissue among whose filaments, are embedded in a

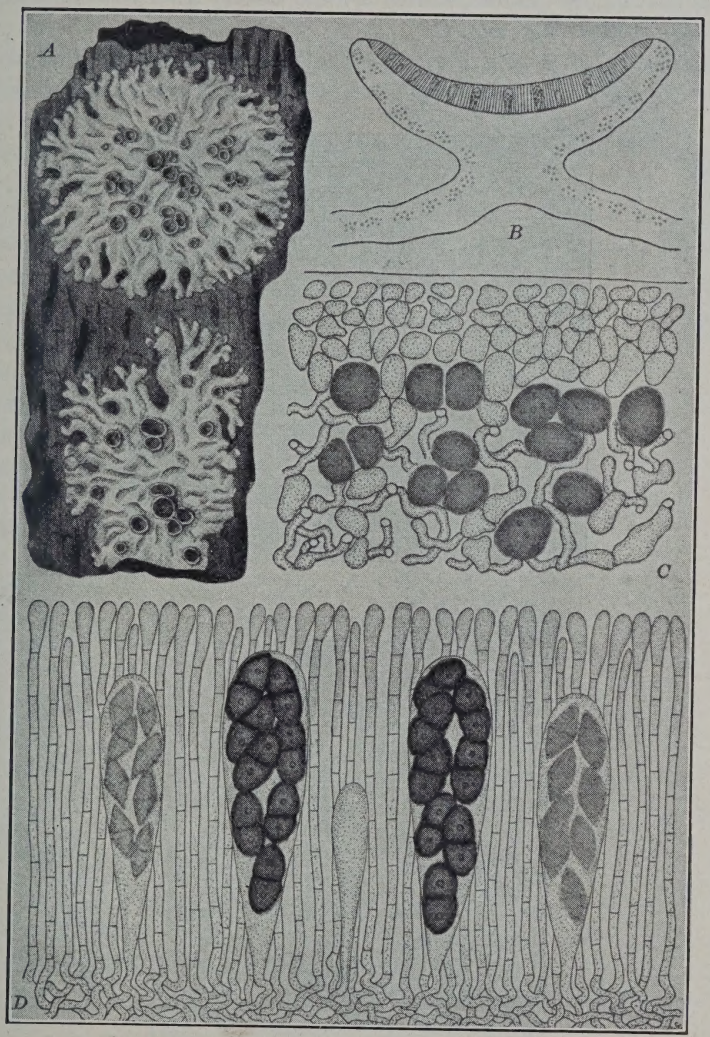
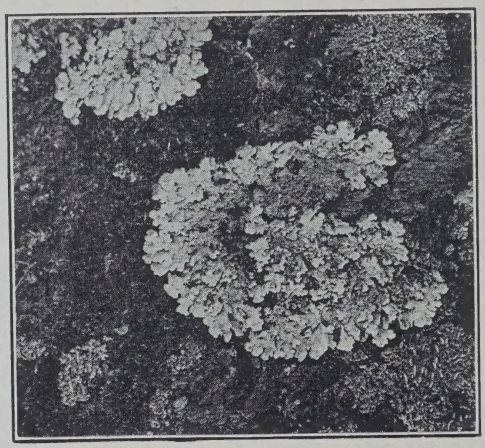


FIG. 277.—A common Tree Lichen (*Physcia stellaris*). A, habit sketch; B, diagram of a vertical section through a spore fruit (apothecium), showing the hymenium, and the position of the algal cells (Protococcus) among the fungal filaments. C, detail of thallus, showing relation of algae and fungus. D, section of the hymenium, with asci in different stages of development and the slender paraphyses. (From Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

definite stratum, the algal cells, here a species of Protococcus. The central part of the thallus consists of more loosely woven filaments forming a sort of pith (Fig. 277, C).

Relation of Alga and Fungus.—The alga found in the thallus of a lichen can and does live in the free state, entirely separate from any



A

B

FIG. 278.—A, foliaceous Lichen, Parmelia; B, crustaceous Lichen on a piece of lime stone.

association with a fungus. It is generally conceded, however, that the fungus is parasitic upon the enclosed algal cells. Some of the latter are penetrated by haustoria of the fungus and injured or killed. In other cases it seems that the fungus obtains nourishment from the alga by

mere contact. Many of the algal cells, apparently uninjured by the fungus, continue to grow and divide. On the whole the algal constituent does not seem to be greatly injured by the fungus, and it is highly probable that it receives some benefit in the protection provided and in the more uniform conditions of moisture and temperature afforded.

The living together of two different species of organisms is known as *symbiosis*. The relation of alga and fungus in the lichen is nutritive, one of the symbionts at least, receiving nourishment from the other. When each symbiont contributes to the welfare of the other, we have *mutualistic* symbiosis.

FIG. 279.—Cladonia, bushy and erect Lichen grown upon poor soil.

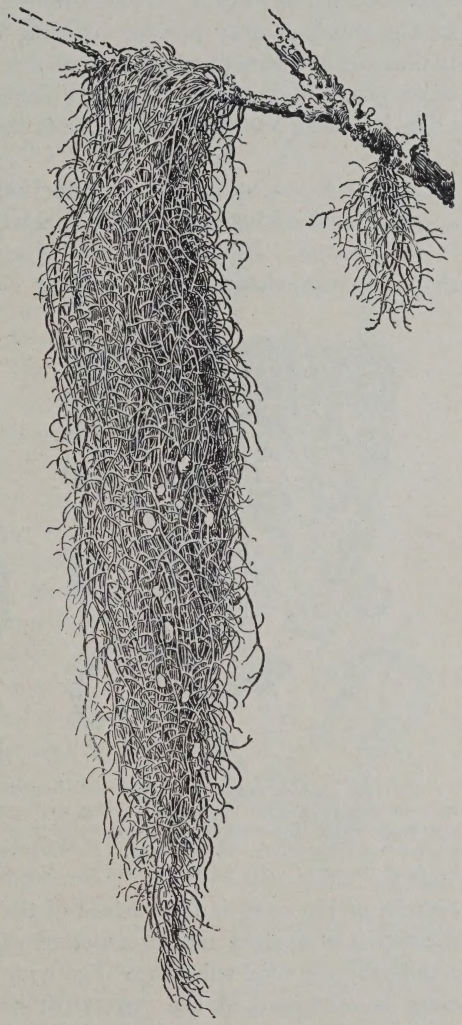


FIG. 280.—Fruticose Lichen, Usnea, hanging from a spruce twig which supports also Parmelia. The Usnea bears disk-like apothecia. (Adapted from Caldwell's "Practical Botany." By permission of Ginn & Company, Publishers.)

In the case of the Lichen under consideration, the status of the alga as stated is that of enforced slavery. Such a relation is styled *helotism* (master and slave).

Vegetative Propagation.—Many lichens propagate vegetatively by the separation from the surface and edges of the thallus of minute proliferations known as *soredia.* These are often so numerous that they appear as a greenish or gray powder covering large areas of the surface of the thallus. Each soredium consists of a few algal cells held in a tangle of short pieces of hyphae. They are readily distributed by the wind and other agencies, and, if deposited in favorable locations, develop into new lichens.

Sexual Reprodution.—The production of fruiting bodies in a lichen is accomplished exclusively by the fungus, the alga taking no direct part in the process. In Parmelia or Physcia the apothecia are small, cup-shaped or disc-shaped bodies slightly elevated above the surface. The

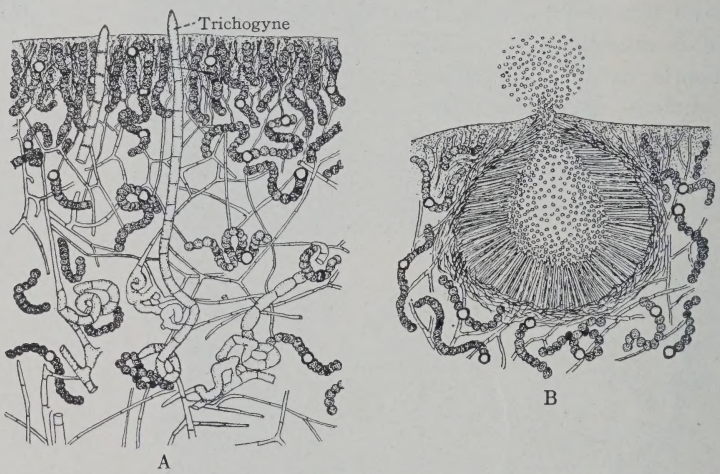


FIG. 281.—Sex organs of a gelatinous lichen, Collema. A, section of thallus, showing the oögonium and trichogyne. One of the cells of the coiled part is the egg. B-spermagonium. Sperms (spermatia) are formed from the ends of very slender hyphae. (A from Kny's chart; after Stahl. B, adapted from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

bottom of the cup, or the surface of the disc, is lined by the *hymenium,* consisting of upright asci interspersed with slender *paraphyses* containing a reddish, oily food substance (Fig. 277, B, D). The wall of the apothecium is composed of the vegetative part of the thallus, consisting of algal and fungal layers. Each ascus contains eight spores, which become two-celled before being discharged.

Lichens are very difficult plants to study structurally, and the origin of the spore-producing part of the apothecium is known definitely in only a few species. It was discovered by Stahl, and later verified by Bauer and Darbyshire, that the sporogenous filaments of the apothecium are developed as the result of a sexual process.

The oögonium is a long multicellular filament, coiled at the base and continued in a straight portion, the distal end of which projects slightly above the thallus (Fig. 281, A). One of the cells of the coiled part represents the egg; the straight part is the trichogyne.

The male gametes are formed in small conceptacles (spermagonia), which open at the surface by means of a small pore (Fig. 281, B). At the ends of slender upright hyphae in the spermagonia small unicellular *spermatia* are cut off. These are equivalent to the sperms of other plants. After being discharged from the spermagonia the spermatia are washed by water to the projecting part of the trichogyne, to which they adhere (Fig. 282, B). The sperm unites with the trichogyne, and its nucleus presumably passes from one cell to another, through small openings in the walls, down to the egg (Fig. 282, A, B). After fecundation numerous sporogenous filaments grow out from the coiled portion of the oögonium, and finally give rise to asci at their upper ends. In the meantime numerous slender hyphae, the paraphyses, grow up among them from the vegetative mycelium near the region of the oögonium. The asci and the paraphyses form the hymenium of the apothecium. The wall of the apothecium is, as has been stated, a vegetative growth of the thallus. The apothecium develops as a closed structure, opening at maturity to form a cup or disc.

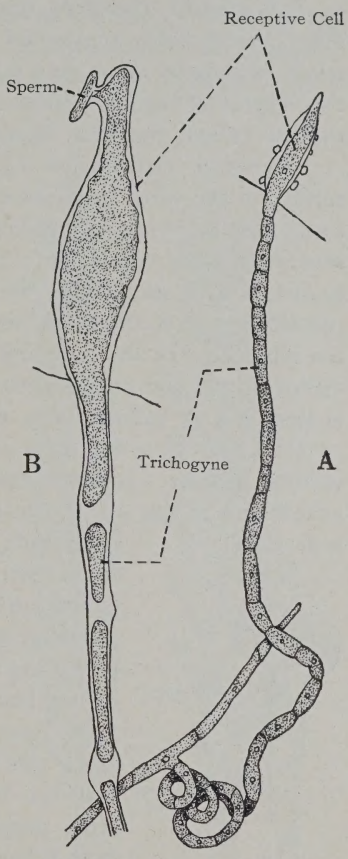


FIG. 282.—Oögonium (carpogonium) of *Collema crispum*. A, the long, multicellular trichogyne ending above the surface of the thallus in a large receptive cell. The egg cell is one of the cells of the coiled portion. B, upper end of a trichogyne with sperm attached to receptive cell. (From Bauer.)

In *Collema pulposum*, according to Bachman, the sperms are not borne in spermagonia, but terminally and laterally on hyphae below the surface. They are, therefore, completely embedded in the thallus and never set free. The trichogyne, consequently, does not grow to the surface of the thallus as described in the foregoing. Its terminal cell, which becomes greatly elongated, grows horizontally towards the region where the sperms are borne, and the union of the sperm and the tri-

chogyne takes place within the thallus. Water as an agency of the transfer of sperms to the trichogyne is doubtless eliminated in species like *Collema pulposum*.

It is evident, therefore, that the spore fruit of the lichen, as in many other Ascomycetes, represents a *spore-producing structure* developed as a result of gametic union, and a surrounding *vegetative part* that arises from the vegetative thallus. In its development the lichen apothecium parallels that in Peziza, Bulgaria, Pyronema, and certain other Ascomycetes.

Geographic Distribution.—Lichens occur widely distributed over the surface of the earth from the tropics to the arctic regions. They live on rocks, tree trunks, etc., and very often in places where conditions are too severe for other vegetation. They are very abundant in moist northern countries such as Alaska, northern Europe, and Siberia. There they constitute one of the more important forage plants for such animals as the reindeer. In the economy of nature also they play the role of rock disintegrators and soil formers. Some lichens are parasitic on the leaves of trees and on various parts of other plants.

Uses to Man.—For ages certain lichens have been used as food by various peoples. Iceland moss (*Cetraria islandica*) is ground up and mixed with wheat and made into cakes. *Lecanora esculenta* was eaten by people in southwestern Asia in ancient times. In eastern Siberia lichens prepared in various ways constitute an important part of the vegetable diet of certain classes of the inhabitants. Poisons, drugs, perfumery, and alcohol have been prepared from certain lichens. From *Roccella tinctoria*, found in the East Indies, on the coast of Africa, and possibly along the northern coast of North America, litmus and the dye, orchil, are derived. Other dyes of blue, purple, red, and crimson are also extracted from lichens.

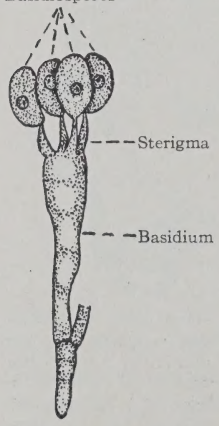


FIG. 283.—A typical basidium. (After Harper.)

BASIDIOMYCETES

In this subdivision of the fungi are included all those Mycomycetes in which certain spores are borne on special cells known as *basidia*. As used in this book a basidium will be understood to consist generally of an elongated cell from whose upper end are produced one or more spores, usually formed at the ends of very slender processes called *sterigmata*. A typical basidium is shown in Fig. 283.

The lower basidiomycetes are represented by the smuts and rusts; the higher representatives include the large fleshy forms like the field

mushroom, puff balls, and stink horns, as well as the woody shelf fungus and the like.

Ustilaginales, Smuts.—The smuts are internal parasites, the mycelium living mostly within the intercellular spaces of the host. They are well known and of great economic importance because of their injurious and destructive effect on the cereal crops and some other economic plants

FIG. 284.—Habit of common smuts. A, Ustilago on corn. B, Tilletia on wheat. C, normal head of wheat.

such as the onion. Although best known on members of the grass family, the smuts occur on species of many other families of plants widely separated in relationship. Most smuts are easily recognized by their black, sooty masses of spores produced in large quantities on various parts of the host plant, as on the stalk, blades, tassels, and ears of Indian corn, and in the heads of oats, wheat, sorghum, etc. (Fig. 284, A, B). Certain

smuts develop the black spores in the anther of the flowers of the host at the expense of pollen grains which are destroyed by the parasite.

Asexual Reproduction.—Two kinds of spores are primarily produced, the smut spores, *chlamydospores*, and the *basidiospores*. In some cases other spores, which will be designated as *secondary sporidia*, are also developed. The sooty masses seen on the host are composed of countless numbers of very small chlamydospores. This spore has a rather thick and firm, dark brown or black wall, which may have various external markings, such as spines or ridges. In some species this spore has one nucleus; in others it may have two. These spores are formed from

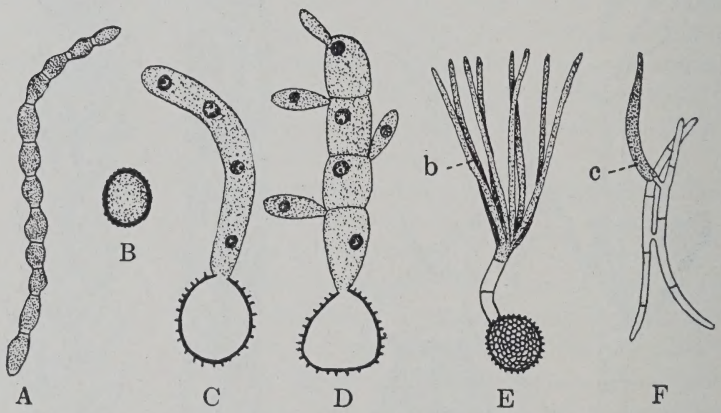


FIG. 285.—The chlamydospore of smut and its germination. A, a piece of hypha forming chlamydospores. B, a single spore. C, D, germination of chlamydospore of *Ustilago scabiosae;* C, the hypha containing four nuclei; D, the hypha divided into four cells, each bearing a basidiospore. E, F, *Tilletia tritici*, stinking smut of wheat; E, basidium produced from a chlamydospore, bearing four pairs of spores, *b*; F, germination of a pair of basidiospores, producing a sickle-shaped secondary sporidium, *c*. (A, E, F after Brefeld; C, D, after Harper.)

undifferentiated hyphae of the mycelium, the short cells of which enlarge, round out, and develop the thick cell wall (Fig. 285, A, B). The spores are scattered by the wind or adhere to the kernels of the threshed grain.

Germination of the Chlamydospore.—In most smuts when the chlamydospore germinates it produces a short hypha usually four cells in length. Each cell produces at its upper end one or more small spores (Fig. 285, C, D). The similarity between this hypha and a typical basidium is the basis for including the smuts in the Basidiomycetes. The whole hypha is regarded as a modified basidium, and the spores that it produces are probably the equivalent of the basidiospores of other

Basidiomycetes.* In general a basidium consists of one cell as stated in the foregoing.

There is, however, much variation in the behavior of the hypha produced by the chlamydospore. Under experimental conditions two or more basidia may be produced from one chlamydospore. In *Tilletia tritici* only the distal cell of the basidium produces spores (Fig. 285, E). These frequently fuse in pairs, and the paired spores germinate forming sickel-shaped secondary spores (Fig. 285, F, *c*). This fusion of spores was formerly supposed to be a sexual fusion, but it is not usually so regarded at present.

On germination the basidiospore or the secondary spore produces an infection tube which enters the seedling as it leaves the seed coat. In the loose smut of wheat no basidiospore is produced, the chlamydospore giving rise directly to the infection tube.

Does Sexual Reproduction Occur in the Smuts?—When grown in culture media under experimental conditions the basidiospores undergo division by budding, producing chains or colonies of cells resembling yeast plants. These frequently unite by a conjugating tube, but there is no fusion of nuclei. Sometimes the adjacent cells of the basidium also unite by a conjugating tube. Until nuclear fusions can be demonstrated in such cases these unions will probably be regarded as merely vegetative fusions having only a nutritive function.

Economic Importance.—Smuts do great injury to the cereals and other crops, and various methods are used in efforts to minimize the damage done. In the case of the oat smut and the stinking smut of wheat the seed grain is treated with formalin to kill the mycelium in the oat hull of the variety possessing hulls or in the grain, and the adhering smut spores in the wheat. For the loose smut of wheat, in which the mycelium is already in the grain, infection having taken place in the flower, the hot water treatment has been used with success.

Selection of seed, and the development of resistant varieties through plant breeding are other means of attack.

In corn smut, treatment of the seed is useless, because the spores responsible for infection pass the winter in the soil.

UREDINALES—RUSTS

The rust fungi have received their common names from their appearance at certain times, when their bright orange or red spores resemble iron rust. These fungi are of great economic importance because of their

* In the older literature, when this relationship was not evident, the short hypha produced from the chlamydospore was spoken of as the *promycelium*, and its spores as *sporidia*.

destructive effects upon their hosts, many of which are plants useful to man. They are also of unusual botanical interest because of their complicated life histories and the problems which the life histories present.

In the complete life history of some species as many as four kinds of functional spores may be produced, and more than one host may be involved. The different stages of the same species,—growing on different hosts, or in different seasons,—resemble one another so little in some cases that they have been regarded in the past as different species of fungi. In other species fewer than four kinds of spores may be produced, and often only one host is required.

The Black Stem Rust* (*Puccinia graminis*).—As a concrete illustration of a rust fungus with a long and complicated life history, the classic *Puccinia graminis* is selected. This fungus is variously known in different localities as Wheat Rust, Red Rust, Black Stem Rust, or Grain Rust. Its two host plants are the tall barberry (*Berberis vulgaris*) and some species of grass, such as wheat, and barley. Four distinct phases of the parasite's life history may be recognized.

Uredinial† *Stage on the Wheat.*—The presence of the uredinial phase of the rust on this cereal may be recognized by the development of numerous orange-colored pustules upon the stem, sheath or blades of the leaves (Fig. 286, A). Each of these is a *uredinium*, which has been formed beneath the epidermis, from the mycelium growing in the intercellular spaces of the host, and which contains numerous *urediniospores*.

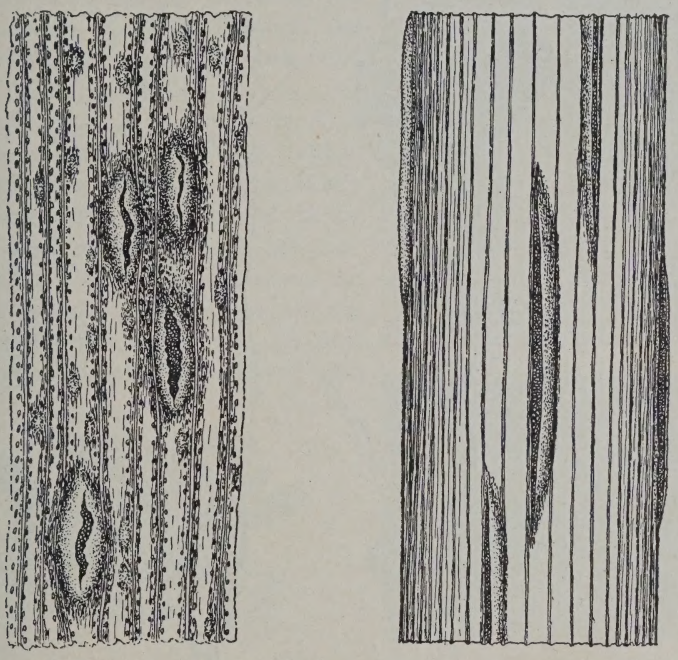
The *urediniospores* are developed singly at the ends of upright hyphae. Each spore has two nuclei, and a thick cell wall variously marked externally and provided with thin places known as *germ pores* (Fig. 287, A). There are usually four germ pores in the region of the equator of the spore. The color is due to reserve food in the form of a reddish oily substance. Urediniospores blown to other host plants germinate and infect them immediately, and a new crop of the same kind of spores may be produced in a few days (B). In this way a large acreage may be infected in a week or ten days of favorable weather.

Telial Stage.—Later in the season, often as the host plant is approaching maturity, the uredinial phase of the rust gradually changes into the

* Not to be confused with the wheat leaf rust *Puccinia triticina*, whose aecial stage occurs on the Ranunculaceae.

† Throughout this discussion the terminology used will be that of the modern literature on the rusts. Some of these terms, with their equivalents in the older literature, are as follows: uredinium = uredosorus; urediniospore = uredospore; telium = teleutosorus; teliospore = teleutospore; basidiospore = sporidium, spring spore; aecium = aecidium; aeciospore = aecidiospore; pycnium = pycnidium = spermagonium; pycniospore = spermatium.

telial phase. The latter is characterized by dark brown or black pustules (*telia*) on various parts of the host, especially the leaf sheaths and the stem (Fig. 286, B.) In this phase the rust is most destructive when it occurs on wheat. This is the dreaded Black Stem Rust. The telia contain thick-walled, two-celled *teliospores* (Fig. 288). Each cell of this mature spore has a single nucleus. At the time of the transition from the uredinial to the telial phase both urediniospores and teliospores may be found in the same sorus (Fig. 287, A).



A B

FIG. 286.—*Puccinia graminis.* A, portion of leaf of wheat with uredinia. B, portion of stem of wheat with telia.

Basidial Stage.—The teliospore is a resistant structure, remaining dormant during the winter in the old straw, or on the ground. On germination in the following spring each of its cells puts out a short hypha four or five cells in length (Fig. 287 C). Each cell of this hypha produces a small spore on a slender stalk. Formerly this hypha was known as a promycelium, and its spores as sporidia, or spring spores. Because of the similarity between the promycelium and certain structures to be discussed later, it is now generally regarded as a *basidium.* The spores which it produces are, accordingly, *basidiospores*, and the stalks on

which the spores are borne are *sterigmata*. No host is required for the production of basidiospores.

Aecial Stage.—The basidiospores are scattered by the wind, and, in so far as is known at present, they can infect no plant but the tall barberry (*Berberis vulgaris*) or some of its near relatives. It is interesting to note, however, that the Japanese barberry (*B. thunbergii*) so much used as an ornamental shrub, is immune. Infection of the barberry takes place

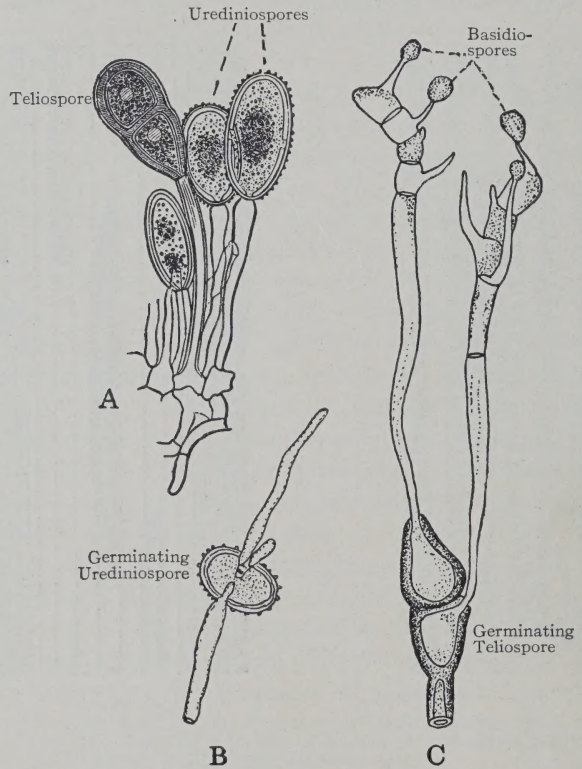


FIG. 287.—*Puccinia graminis*. A, portion of a uredinium, showing urediniospores and one teliospore. B, germinating urediniospore. C, germinating teliospore, with basidiospores. (A and B, after DeBary; C, after Tulasne.)

in the early spring, and yellowish blotches soon appear on its leaves. On the lower side of the leaf in each of these blotches clusters of minute cups (*aecia*) will soon burst through the epidermis, and the corresponding upper surface will be marked by minute black dots, which are the openings of small cavities (*pycnia*) formed beneath the epidermis (Fig. 289, A, B).

The aecia are filled with orange-red *aeciospores*, which are blown away to the proper grass plant, in this case the wheat, to give rise to the ure-

dinial phase again. The pycnia produce numerous small spore-like bodies, *pycniospores*.

Details of the aecial phase are best seen in vertical sections through a diseased spot of the leaf of the host, where hypertrophy occurs to such an extent that the leaf is two or three times its normal thickness.

The aecium has a definite wall of fungal tissue. It is formed beneath the epidermis, but at maturity the accumulation of spores ruptures the epidermis (Fig. 290). The wall of the cup is also ruptured at the top, and its edge curves outward. Chains of *aeciospores* are borne on erect hyphae arising from a weft of mycelium in the bottom of the cup. In each chain the spores alternate with small, flattened intercalary cells. The spores and the intercalary cells are binucleate, but the mycelium from which they are produced is made up of uninucleated cells.

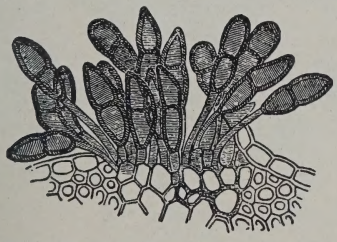
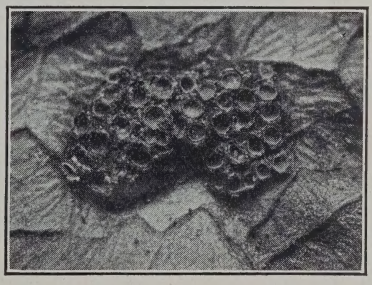


FIG. 288.—A vertical section through a telium. (After DeBary.)

A



B

FIG. 289.—*Puccinia graminis*. A, leaves of barberry, showing clusters of aecia. B, a cluster of aecia magnified.

The pycnia are small, flask shaped cavities whose walls are covered with erect hyphae from which the pycniospores are cut off (Fig. 290). They appear in advance of the aecia of the same diseased spot. For some years students of the rusts, as a rule, have looked upon the pycniospores as functionless male gametes, the pycnium representing an antheridium in the phylogenetic history of the fungus, and now functionless.

It has been claimed recently that if the pycniospores produced upon one diseased spot are transferred to another spot whose mycelium is presumably of a different sex, they will germinate and the resulting

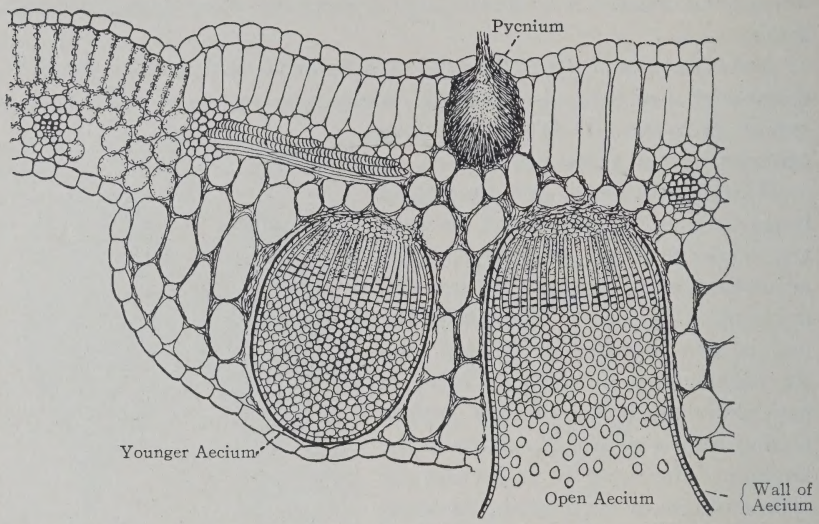


FIG. 290.—Cross section of portion of leaf of barberry including a portion of a spot infected with Puccinia. The extent of the hypertrophy may be seen in comparison with the normal condition of the leaf as shown at the left. (Diagrammatic.)

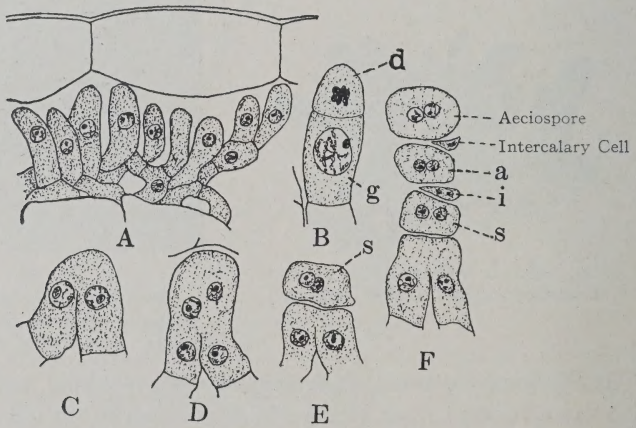


FIG. 291.—*Phragmidium speciosum* on *Rosa humilis*. Early stages in the formation of the aecium and aeciospore. A, upright hyphae under the epidermis. B, division of the end cell of a hypha into an upper, sterile, transitory cell (*d*), and a basal cell (*g*), the gamete. C, union of the two gametes. D, later stage, following first nuclear division. E, abstriction of the first aeciospore initial cell (*s*). F, row of binucleate aeciospores (*a*), separated by partly crushed intercalary cells (*i*); *s*, the last formed spore initial. (Adapted from Christman.)

mycelia will function with the mycelium of that spot in producing the diploid condition.*

Development of the Aeciospores—Indications of Sexuality.—It will be noted that certain cells of this rust have been described as uninucleate (haploid) and others as binucleate (diploid). This occurrence is generally interpreted as a manifestation of sexuality. The details, which have been

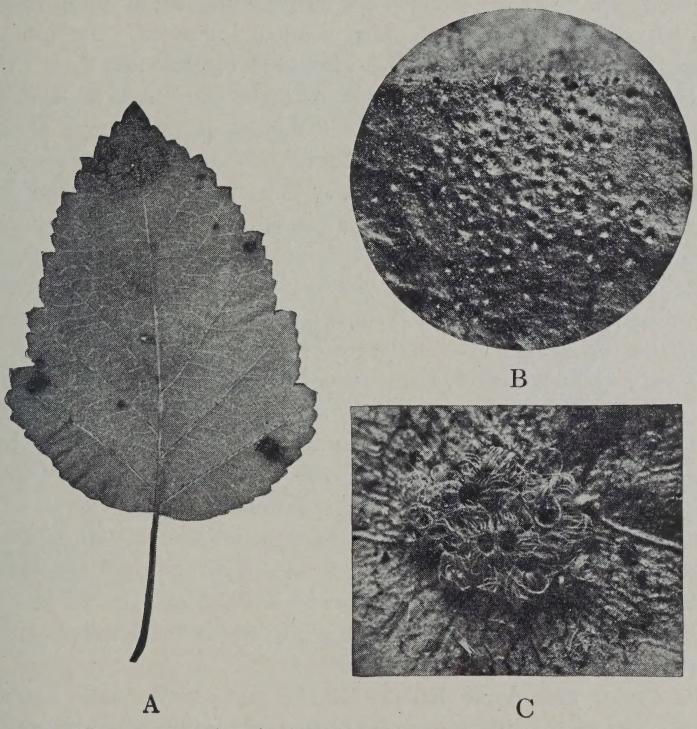


FIG. 292.—*Gymnosporangium juniperi-virginiae.* A, leaf of wild crab apple showing spots of infection. B, diseased spot as seen from the upper side of leaf, showing openings of the pycnia. C, open aecia as seen on lower side of leaf.

investigated in a few rusts, and are supposed to be of general occurrence, may well be described as it has been reported in a species of Phragmidium.

The mycelium of the aecial stage is made up of uninucleate cells. The aecium begins in a weft of hyphae formed beneath the epidermis. From this weft grow up side by side a number of club-shaped cells, each containing a nucleus (Fig. 291, A). Each club-shaped cell now divides into a small distal cell and a large basal cell (Fig. 291, B, *d*, *g*). The distal cells (*d*) disorganize and become crushed out. The basal cells elongate

* It has been asserted also that the pycniospores function as sperms, and that they unite with trichogynes which project through the epidermis.

slightly and assume the general character of gametes, fusing in pairs. They elongate slightly and fuse at the upper ends (C). The united ends continue growth as a single hypha (D). The nuclei pass into the new portion and remain associated, side by side, but do not fuse. They now divide simultaneously, and a cell is cut off containing two of the daughter nuclei lying side by side, the other daughter nuclei remaining in the cell below (Fig. 291, D, E). The cell cut off (*s*) is the initial cell of the aeciospore. It divides transversely into a small lower cell, the intercalary cell, and a large upper cell, the aeciospore (Fig. 291, F, *i*, *s*). In the meantime the fused end of the two gametes increases in length, and another aeciospore-initial is cut off. It divides in turn into an aeciospore and an intercalary cell, and the process continues, resulting in a row of aeciospores and alternating intercalary cells. From the foregoing it is evident that the two nuclei in each are not sister nuclei, since they were derived from two separate cells regarded as gametes.

The binucleate condition of the cells of the mycelium developed from the aeciospores continues through succeeding stages until the formation of the teliospore. The teliospore initial, which is cut off from the end of an upright hypha, is binucleate. Its two nuclei divide simultaneously, the two spindles lying closely side by side. When the daughter nuclei reach their respective poles they unite, and the two spindles become as one. Cell divisions follow, giving rise to the several celled teliospore, each cell being binucleate but finally containing a single nucleus. This condition continues until the formation of the aecium. The basidiospores developed from the teliospores are, therefore, uninucleate, and the mycelium developed from them is likewise uninucleate, i.e., haploid. The mycelium with uninucleated cells is regarded as the haploid structure; that with binucleated cells, the diploid.

The Cedar and Apple Rust.—Of the many rusts with shorter life histories, one of the best known is *Gymnosporangium juniperi-virginianae* Schw. Two hosts are involved in the life history, but the uredinial stage is lacking. The aecia are borne on the leaves of the apple tree, or some of its near relatives as the haw (Fig 292); the teliospores are produced on the juniper tree, more commonly known as the red cedar.

The aeciospores are carried from the apple tree to the juniper by the wind. The presence of the mycelium in the leaves of the juniper causes an hypertrophy, resulting in the formation of large, brown, leathery galls known as "cedar apples" (Fig 293). These galls may attain the size of a hen's egg, although many remain small, and several may be found on a single twig.

In the "cedar apple" which is composed of large, thick-walled cells of cedar tissue, the mycelium spends the winter. The numerous small

depressions in the surface indicate the position of developing telia. The teliospores mature in the spring (April, May in Indiana) and after a rain or protracted period of moist, warm weather, long gelatinous columns of teliospores grow out from these depressions (Fig. 293). One of these masses is shown enlarged in Fig. 294. The teliospores borne on long slender pedicels germinate in this jelly, and the basidiospores resulting are carried by the wind to the leaves of the apple tree.

FIG. 293.—*Gymnosporangium juniperi-virginiae*. Galls, ("cedar apples") formed by the rust on leaves of juniper. At the right a "cedar apple" in winter condition. At the left, the same after the elongation of the columns of teliospores in the spring.

Some Other Rusts.—A more simple life history is seen in *Puccinia malvacearum* Mont., a rust of the common hollyhock. Only two stages occur, the telial and the basidial, and only one host is involved.

A very conspicuous rust, *Gymnoconia interstitialis* (Schlecht.) Lagerh., imparts an orange-red color to the leaves of the blackberry plant, the spore masses sometimes almost covering the lower sides of the leaves. The aeciospores here are borne in a broad cup, known as a *Caeoma*, which has no definite wall of fungal tissue. The aeciospores sometimes produce a structure much like a basidium, thus resembling teliospores.

The very destructive rust, *Cronartium ribicola* Fisch. de Waldh., has its aecial stage on the white and other five-needled pines and the uredinial and telial stages on species of gooseberry and currant. This rust is known as the white pine blister rust.

Methods of Control of Rusts.—In order to diminish the ravages of rusts upon crop plants and forest trees various methods have been

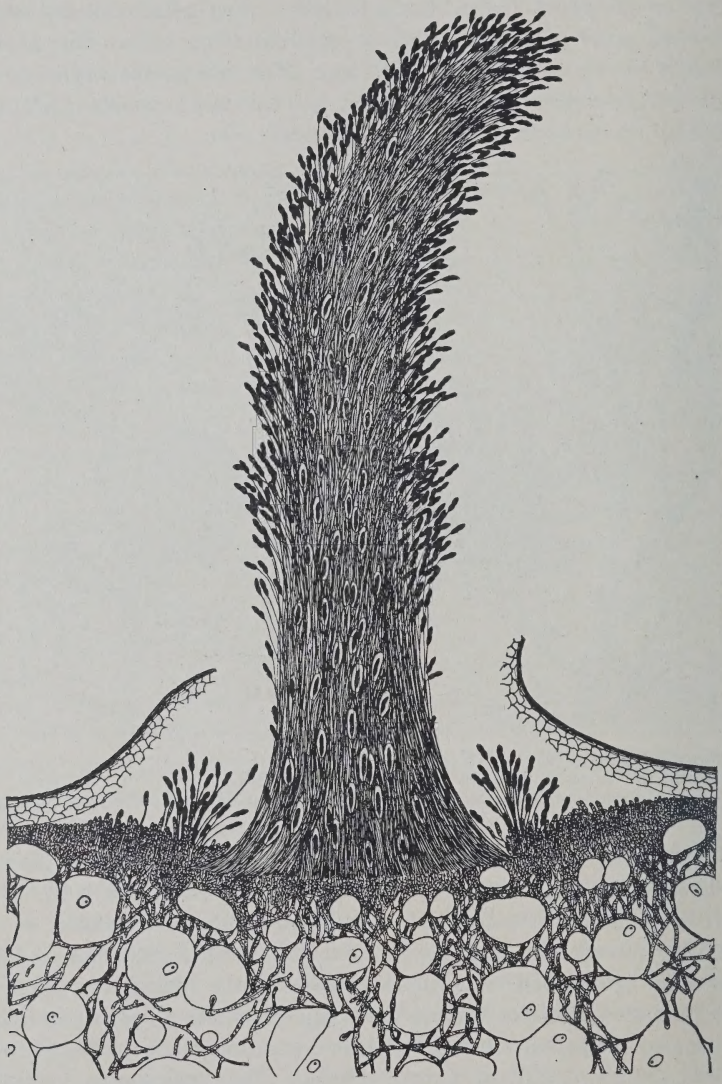


FIG. 294.—*Gymnosporangium juniperi-virginiae.* A, longitudinal section of a column or spike of teliospores emerging from beneath the cortex of the "cedar apple." (After Reed and Crabill. From Bull. No. 9 of the Virginia Agricultural Experiment Station.)

employed, all of which are based upon an understanding of the complete life history of the fungus.

In species like the cedar and apple rust in which the spores produced upon one host infect some other host, the host of lesser economic importance is destroyed in a locality of greater or less extent. If the growing of apples be of greater importance in a locality than the production of cedar trees, the cedar trees may be destroyed, or, if practicable, all "cedar apples" may be gathered in autumn or winter and destroyed.

In regions where the white pine timber occurs or is cultivated extensively, the gooseberry and current bushes are destroyed. In like manner the destruction of the tall barberry in regions where this shrub is infected by the rust, has done much to lessen the damage caused by the parasite and to increase the yield of wheat.

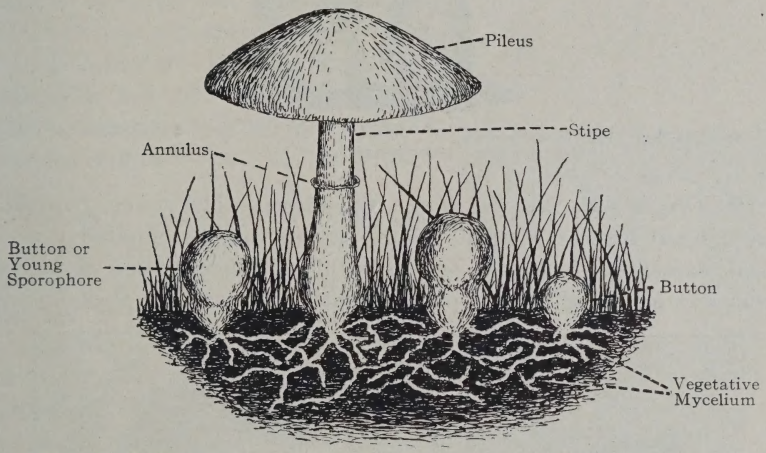


FIG. 295.—Diagrammatic habit sketch of field mushroom, showing the mycelium in the soil and sporophores in different stages of development.

In case the parasite cannot be destroyed or its dispersal be prevented, the remaining hope is to produce, by breeding, more resistant varieties of the desired crop plants.

There is still much to be learned concerning the rust fungus, that even beginners may think about. For example, why is the tall barberry so susceptible to infection by *Puccinia graminis* while the Japanese barberry is immune? Digging up tall barberry bushes will not alone solve the rust problem.

The Field Mushroom (*Psalliota campestris*).—The field or meadow mushroom is representative of a large class of typical basidiomycetes. The entire plant body of the mushroom, like other fleshy fungi, consists of two parts, the *vegetative mycelium* living in the substratum, and the *sporophore*, or spore-producing part, which is usually found above the surface of the substratum (Fig. 295).

The vegetative part consists of numerous mycelial strands and cords which spread among the particles of the soil, from which nourishment is absorbed.

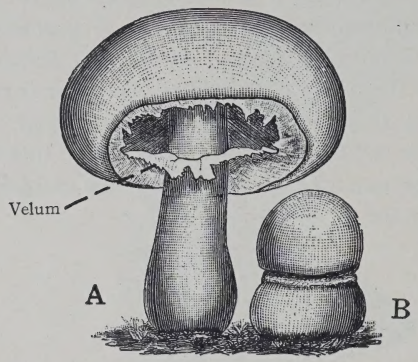


FIG. 296.—Adult sporophore and a "button" of the field mushroom (*Psalliota campestris*).

The Origin and Structure of the Sporophore.—The young sporophore is recognized first as a small, white, opaque, undifferentiated mass of fungal filaments, which soon reveals within a differentiation of the two main parts of the adult sporophore, namely, the stalk, or *stipe*, and the

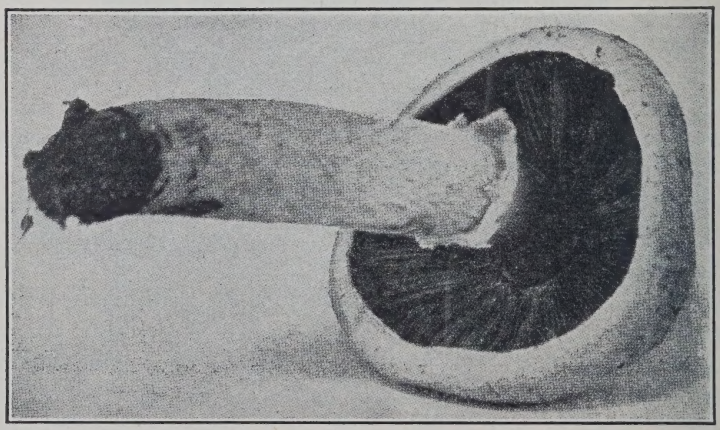


FIG. 297.—*Psalliota campestris*, showing "gills" on underside of pileus, and the annulus encircling the stipe. (After Atkinson.)

cap, or *pileus*. These younger stages of development of the sporophore are often spoken of as "buttons" (Figs. 295). A longitudinal section of a "button" reveals the central stipe, bearing at the top the pileus folded down like a closed umbrella. A delicate membrane connects the edge of

the pileus with the stipe. This is the inner veil, *velum* (Fig. 296, A). On the underside of the pileus are developed numerous thin, flat spore-bearing *lamellae*, more commonly known as the "gills" (Fig. 297).

When the sporophore is mature, the stipe elongates rapidly, and the pileus opens out, the whole structure resembling an open umbrella. The veil is broken loose from the edge of the pileus and remains as a ring around the stipe when it is known as the *annulus*.

Viewed from the under side of the pileus, the gills are seen to be thin, flat plates radially arranged and fastened edgewise to the pileus. A tangential section of the pileus bears some resemblance to a comb, the gills corresponding to the teeth (Fig. 298, B). In a cross section of the closed pileus the gills appear arranged somewhat as the spokes in a wheel.

The stipe and pileus are composed of closely compacted hyphal filaments and closely set shorter cells that form a false tissue, *pseudoparenchyma*.

The Gill and the Hymenium.—The entire surface of the gill is covered by the hymenium; the central part of the gill is the *trama*. The relation of the two is clearly seen in a cross section, as shown in Fig. 299. The hymenium is composed of two kinds of cells, the longer being the *basidia*, and the shorter, the *paraphyses*. Each basidium bears at its free end normally four spores on slender *sterigmata*. Each basidiospore is uninucleate (Fig. 300, E, *s*). The central part of the gill, the trama, consists of loosely interwoven, septate hyphae, most of which terminate in basidia or paraphyses.

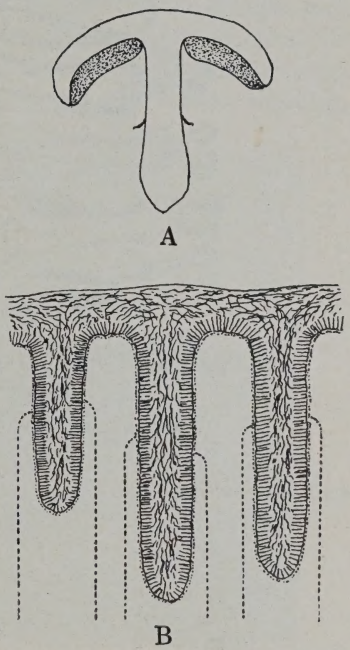


FIG. 298.—Sporophore of Field Mushroom (*Psalliota campestris*). A, outline of a longitudinal section through sporophore; the shaded parts are the "gills." B, tangential section through a portion of pileus; the dotted lines indicate the trajectories of the spores after being shot off from the basidia.

Dispersal of Spores.—Spore dispersal in the field mushroom is accomplished by the wind. The mature spores are ejected forcibly from the sterigmata and thrown clear of other basidia. They fall freely between the gills, which are kept in a vertical position by the geotropic response of both the stipe and the gills. The trajectories of the spores are shown by the dotted lines in Fig. 298, B.

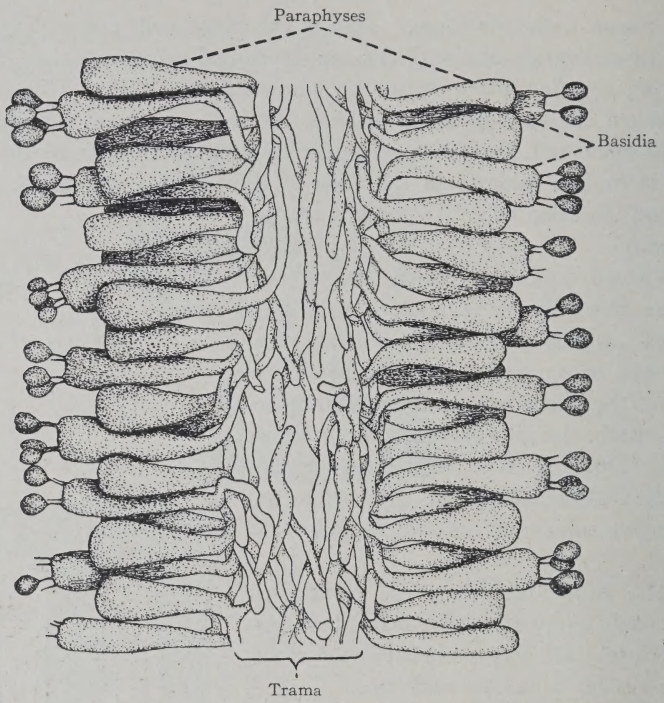


FIG. 299.—Portion of a cross section of a "gill," showing trama in the center and the hymenium on either side.

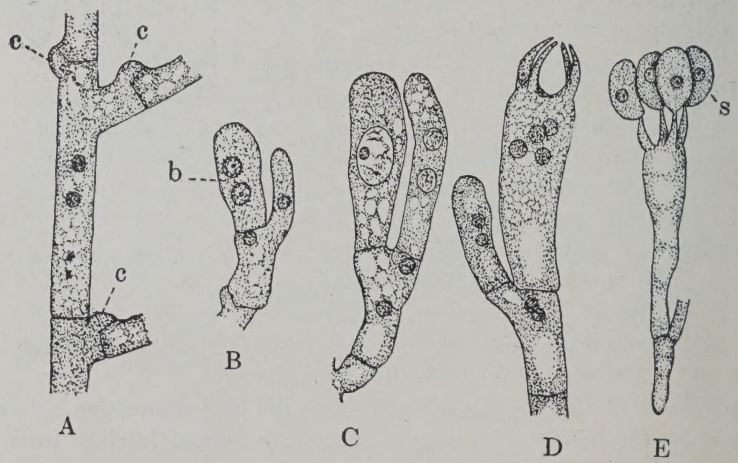


FIG. 300.—*Hypocynus subtilis*. Clamp connections and formation of basidium. A, binucleate cell and characteristic clamp connections (*c*). B, young basidium (*b*), and a younger basidium budding out from stalk cell. C, two young basidia, in one of which the two nuclei have united. D, two basidia, the larger containing four spore nuclei and having four sterigmata already formed. E, mature basidium with four basidiospores borne on the sterigmata. (From Harper.)

Development of the Basidium.—The initial cell of the basidium contains two nuclei, which soon fuse (Fig. 300, B, C). With further growth, the fusion nucleus gives rise, by two successive divisions, to four nuclei. In the meantime the four slender sterigmata have grown out of the distal end of the basidium (Fig. 300, D). The end of each sterigma enlarges to form the spore, into which a nucleus passes (E, *s*).

Origin of the Binucleate Cells.—The initial cells of the basidia, and the cells from which they spring, are binucleate. The mycelium developed from the basidiospores is at first uninucleate. Later in development, adjacent cells of the hyphae are united by a so-called *clamp-connection*,

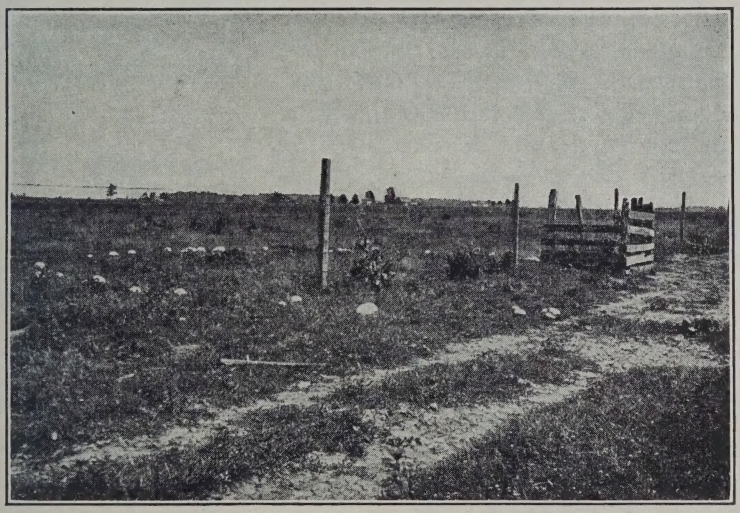


FIG. 301.—Fairy Ring of the giant puffball (*Calvatia maxima*). (From a photograph by P. Weatherwax.)

and through this connection the nucleus of one passes over into the other (Fig. 300, A).

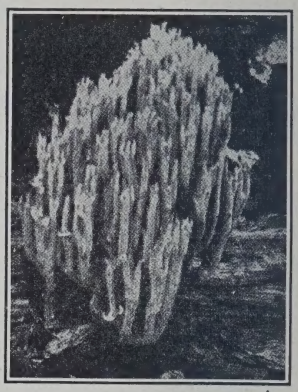
The Fairy Ring.—In pastures and grassy fields the field mushroom and other species of mushrooms may exhibit the phenomenon known as the fairy ring. A fairy ring consists of a number of sporophores appearing above the surface of the ground in the form of a circle. The circles may vary from one-half meter or less to three or more meters in diameter (Fig. 301). Sometimes the rings form a regular and complete circle, but frequently incomplete rings result.

The mycelium of the field mushroom (*Psalliota campestris*) as well as that of some other mushrooms is perennial, living in the soil for several years. The fairy ring is, consequently, a living zone of mycelium which

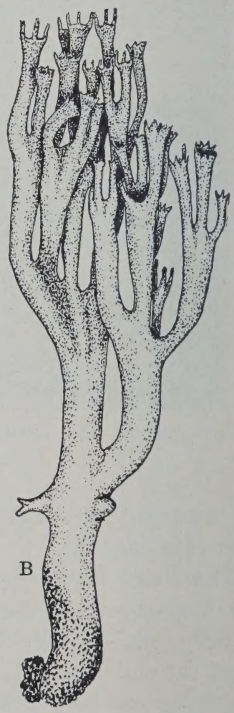
develops centrifugally. The actively growing outer edge of this zone develops sporophores from time to time which appear, therefore, in a ring.

It is possible that the ring of mycelium may have had its origin in a small circular area of mycelium which began to die in the center, the oldest part. Then by continued growth in a radial direction at the circumference an ever widening circle of mycelium is formed; and by continued death and decay of the older parts of the mycelium a progressively larger central area devoid of mycelium will result.

Coprinus.—Two common mushrooms found in well fertilized lawns and fields in spring and summer are the Shaggy Mane (*Coprinus comatus*) and the Ink Horn (*Coprinus atramentarius*) (Fig. 302). These are edible if used before they turn black. In both species when the spores are



A



B

FIG. 303.—A, Coral Fungus, Clavaria. B, portion of sporophore ×3.

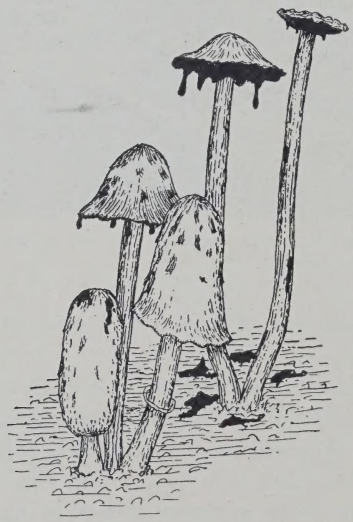


FIG. 302.—*Coprinus comatus*, Shaggy Mane mushroom; one unopened sporophore and four opened; in the mature sporophore the digested parts of the gills fall away as drops of inky-black fluid after the spores are released. The spores are dispersed by the wind.

mature, portions of the gills from which the spores have fallen, and the

adjacent parts of the pileus undergo autodigestion, the resulting liquid falling to the ground in inky black drops. The spores ripen first at the

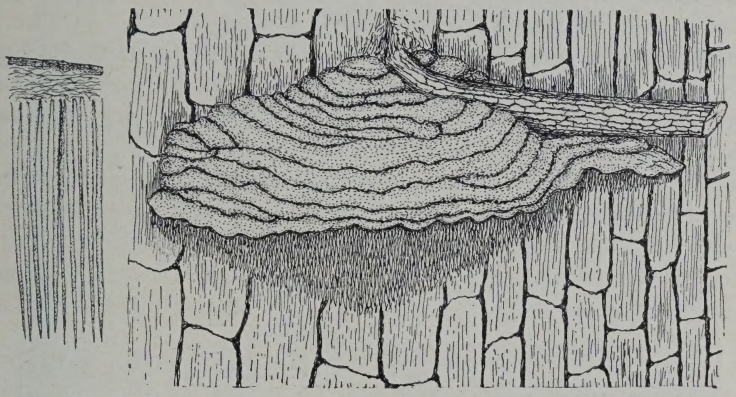


FIG. 304.—Hydnum. Sporophore attached to the bark of a pine tree. At the left a few pendant spikes enlarged.

outer ends of the gills, the process proceeding toward the stipe. The removal of the spore-free material by deliquescence facilitates dispersal, which is accomplished by the wind.

FIG. 305.—A pore-mushroom, Boletus. (From Bergen and Davis.)

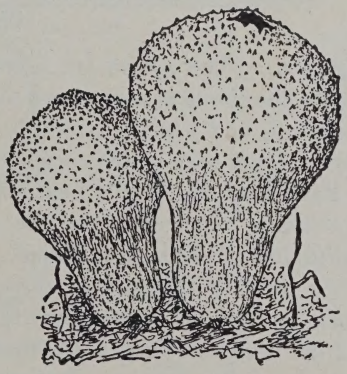


FIG. 306.—A puffball, Lycoperdon. (From Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

Clavaria.—The sporophore of Clavaria consists of numerous upright, somewhat club-shaped or flattened, simple or much branched spikes,

which bear the hymenium on their surfaces. The spikes are united at the base (Fig. 303).

Hydnum.—In the sporophore of Hydnum spore-bearing spines hang vertically from the pileus-like structure (Fig. 304).

Boletus.—Many species of Boletus resemble the umbrella-shaped mushrooms. Here there are numerous pores opening on the under side of the pileus. Each pore is the opening of a tube-like cavity whose inner surface is covered with the hymenium (Fig. 305).

Fomes.—The large and familiar woody shelf fungi, Fomes and Polyporus, are also pore-fungi, the pores opening on the under side of the sporophore. Fomes is perennial.

Lycoperdon.—The puffballs (Lycoperdon, Calvatia) include some of the largest fleshy fungi, often measuring 40 cm. or more in diameter

FIG. 307.—Earth Star, Geaster.

(Fig. 306). The spores are borne in numerous closed cavities. When mature the tissue of the sporophore dries out and the rind is ruptured or breaks off, and a slight stroke or a puff of wind will set free millions of spores, which may be blown for long distances.

Earth Star, and Bird's Nest Fungi.—Among interesting basidiomycetes of common occurrence are the species of Geaster (Earth Stars) and Crucibulum (Bird's Nest Fungi). The Earth Star develops entirely or partly beneath the surface of the soil or other substratum (Fig. 307). When mature the outer covering (peridium) splits radially at the top, and the segments turn back, thus exposing and lifting the spore-bearing part above the surface. In some species the spore-bearing part is prolonged at the top into a nozzle-shaped protuberance.

The Bird's Nest fungus is common in summer in fields and lawns fertilized with barnyard manure and upon old sawdust. The open sporophore resembles a nest with eggs. The "eggs" are the special bodies in which the spores are produced (Fig. 308).

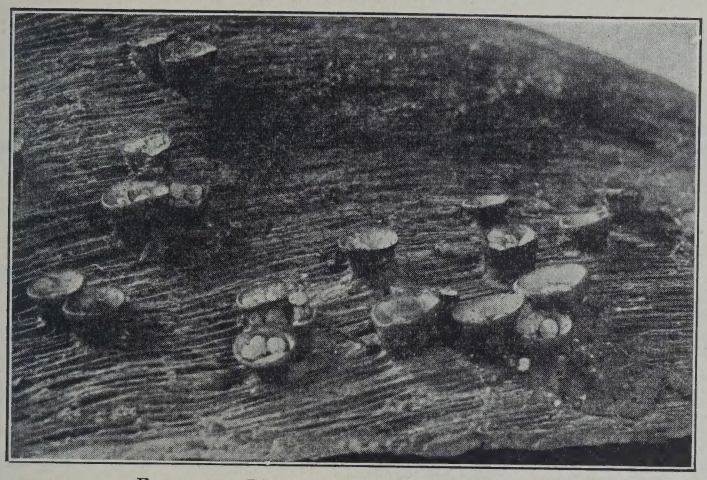


FIG. 308.—Bird's Nest Fungus (Crucibulum).

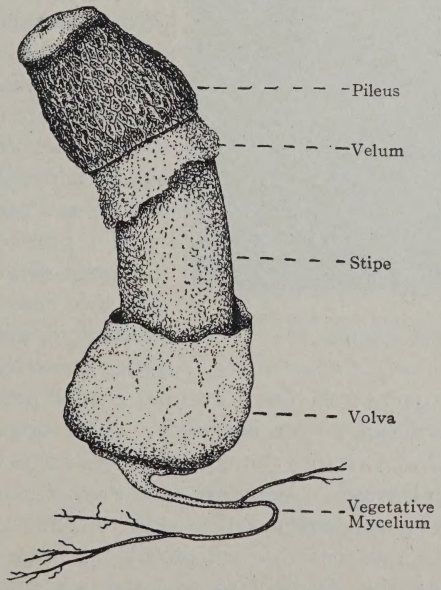


FIG. 309.—Stink-Horn or Carrion Fungus (*Dictyophora duplicata* (Bosc.) Fischer). Adult sporophore with small portion of underground mycelial cord.

Stink Horn.—Perhaps the most highly specialized fleshy fungi are the Stink Horns, (Phallus, Dictyophora) which owe their name to the unpleasant odor liberated when the spores are mature (Fig. 309). The spores are surrounded by a sweetish, sticky, ill-smelling fluid attractive to flies, which are among the agencies of spore dispersal.

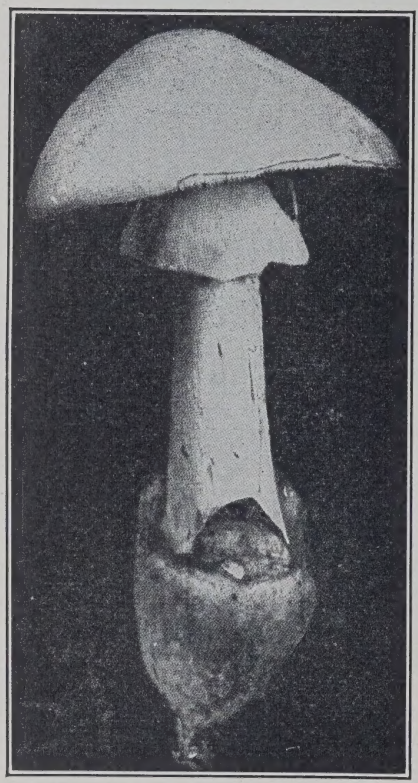


FIG. 310.—The poison *Amanita phalloides*. (After Atkinson.)

Many mushrooms are brightly colored, especially some of the very poisonous species. One of the largest and perhaps best known mushrooms is the poison *Amanita phalloides*, sometimes referred to as the "poison cup," "death cup" or "death angel" (because some forms are white) (Fig. 310).

Fungi Cultivated by Ants.—Certain species of tropical or subtropical ants of America are known to cultivate and propagate fungi as a source of food in the cavities of their subterranean nests. They prepare the substratum for their mushroom beds wholly or in part from organic material brought in from the outside. This often consists of bits of material cut from the leaves of trees and carried long distances.

Not only do the ants care for the fungi within the nest, but they establish new gardens by planting mycelia in new nests. When the young queen leaves the parental nest to start a new colony she takes with her a small pellet of living mycelium mixed with scrapings from her body. After preparing a small cavity in the ground and closing the entrance, she starts a new fungus garden and begins to lay eggs. When the larvae are large enough to need food, the mycelium has made sufficient growth to support them.

The insects apparently do not permit the fungi to form sporophores, but encourage the development of the mycelium. Tiny, knob-like proliferations, consisting of the enlarged and rounded ends of hyphae, are the parts used for food. Sporophores found in a deserted nest have made it possible to identify the fungus cultivated by one genus of ants as the

Basidiomycete, *Rozites ganglyophora*. That this is the species used for food is evident from the fact that spores from this mushroom gave rise to mycelia similar to that found in the nests of the ants.

Summary.—1. Fungi form a striking contrast to the algae in being without chlorophyll. They cannot make their own food. They are, therefore, consumers and not producers. Their food consists of organic matter, living or dead.

2. Structure and reproduction are similar to those in the algae, as in Albugo and Vaucheria.

3. When parasitic forms produce a diseased condition they are called *pathogenes*.

4. Parasites known as rusts, smuts and mildews are destructive to economic plants grown by man.

5. Some of the fleshy fungi, such as morels, truffles, and the field mushrooms are edible, ranking among the rare delicacies of the table. Others are deadly poison. No one should eat mushrooms unless he knows definitely that they are not poisonous. There is no safe rule for the inexperienced person.

6. Three great subdivisions may be recognized: *Phycomycetes*, *Ascomycetes*, and *Basidiomycetes*. As a rule, the Phycomycetes have tubular mycelia. Common forms are the bread mould (Rhizopus), and water moulds (Saprolegnia), and "white rusts" (Albugo). In the Ascomycetes, the spores developed directly or indirectly from the zygote are borne in asci. Examples are mildews, disc fungi, and morels.

7. A striking parallel is to be found between the Ascomycetes and the Rhodophyceae in the development of the spore-fruit. In both groups the germinating zygote results in the formation of sporgenous filaments which produce the spores. The wall of the perithecium in the mildew is developed in the same manner as the wall of the cystocarp in the red alga, Polysiphonia.

8. The distinguishing characteristic of the Basidiomycetes is the production of spores upon basidia. Representative forms are rusts, smuts, mushrooms, puff balls.

9. A lichen is a combination of a fungus and an alga. The fungus is chiefly an ascomycete.

10. Fungi Imperfecti produce conidia only. Those fungi known as Mycelia Sterilia do not bear spores at all. They exist in the form of mycelia alone.

TOPICS FOR REVIEW AND DISCUSSION

How are algae distinguished from fungi?

Explain the terms, *parasite*, *saprophyte*, *pathogene*, *hypha*, *mycelium*.

Do you know of fungi which may live both as parasites and saprophytes?

Why are the Phycomycetes referred to as algal-fungi?

Distinguish the Phycomycetes and the Eumycetes in regard to the structure of the mycelia.

A piece of moist sterilized bread exposed to the air of the room five minutes then kept in a moist warm place will, in a few days, become covered with Rhizopus. Explain.

What are stolons in Rhizopus?

Does the mycelium of Rhizopus penetrate the bread?

Explain how the mycelium secures food from the bread.

What is a sporangiophore?

What is the evidence that there are male and female strains of the mycelia in Rhizopus.

Does it enable you to understand Rhizopus better if the signs + and − are used to designate female and male strains respectively?

What kind of mycelia will the spores developed in sporangia of a male strain produce?

If one sows the spores from a sporangium developed upon the hypha produced by the zygote of Rhizopus, how many kinds of mycelia will be secured and in what proportion?

What is the diploid structure in Rhizopus?

Does the zygote of Rhizopus develop a mycelium on germination?

What is a monoecious mycelium? A dioecious mycelium?

What is the "Pilobolus gun"? Is it of any value to the fungus?

Do fungi give a geotropic and a phototropic response?

What is the difference between a sporangium and a conidium?

What is meant by the terms *host* and *parasite* in speaking of fungi?

What are haustoria? What spores produced by Albugo are the infecting spores?

In what form does Albugo spend the winter? How does the fungus get a new start in the spring?

What are internal and external parasites with respect to the host plant?

What are water moulds?

Are they of any economic importance in any well-known industry?

What is the fly mould, Empusa?

Explain what an ascus is.

What is a basidium?

What are Fungi Imperfecti?

Why is the cultivated yeast plant grouped with the Ascomycetes?

When tame yeast feeds upon sugar what are the two by-products?

What uses are made of these by-products by man?

Will yeast grow in the absence of atmospheric air?

Are any kinds of yeast pathogenes?

Is it correct to speak of the perithecia of mildews (Sphaerotheca, Microsphaera) as fruits? Why spore fruits? Are they as truly fruits as apples?

Is the shell or cover of the perithecium haploid or diploid?

Are the conidia of the mildew haploid or diploid?

Are the appendages developed upon the perithecia of any value to the fungus?

Write life cycle diagrams of Rhizopus, Albugo, Sphaerotheca.

Do you know of any rusts like Albugo which are injurious to a field or garden crop?

What parasitic fungus is injurious to the white potato plant?

What methods are used to minimize the ravages of the potato blight or rust?

What is "the black knot" of the plum tree?

What are "peach mummies"? To what fungus are they due? Was this fungus at one time classed with the Fungi Imperfecti? Why?

What is ergot? Is ergot of any economic value?

What is a sclerotium? What spores of the ergot are produced in connection with "honey dew"? Where are these spores developed?

What are "cup fungi"?

What two ascomycetous fungi are delicacies of the table?

What precaution should be taken in selecting mushrooms in the field or woods for food?

What are the two hosts of the stem rust of the wheat?

What is the "cedar apple"? What relation does the "cedar apple" sustain to the leaves of orchard apple trees?

Is the "cedar apple" a real apple? Is the bulk of its tissue cedar tissue or fungal tissue?

What is a gall, botanically speaking?

What methods are taken to minimize the ravages of the stem rust of wheat?

If you owned an apple orchard would you like to have red cedar trees (Juniperus) growing near?

Do the urediniospores and the teliospores of the black stem rust of wheat develop from the same mycelium?

The urediniospores of the black stem rust have been referred to as "repeater spores." Why?

What distinguished rust specialist lives in Indiana?

How many kinds of spores are produced in the smuts?

For what smut is the hot water treatment used? For what smut is formalin used?

Why would the treatment of seed corn for smut be of no value?

What is a Lichen? What is symbiosis? What is the relation of the two symbionts in Lichens?

Are any Lichens parasitic?

What Lichens have long been used as food by human beings?

What is Iceland Moss?

What is litmus and for what is it used?

What are the soredia of Lichens?

What is reindeer moss?

What is the role of Lichens in the economy of nature?

What constituent of the Lichens produce the spores?

Do you know of any plant or plants more widely distributed over the surface of the Earth than are Lichens?

Who was De Bary? To the knowledge of what group of plants was he one of the foremost contributors?

What part of the field mushroom is eaten as food?

Where does the vegetative part of the mushroom grow?

What are *annulus*, *veil*, *volva*, *stipe*, *pileus*, *gills*, and *hymenium* as applied to a mushroom?

What is the "stink horn"? Why does the pileus of the "ink horn" or "shaggy mane" fungus (Coprinus) dissolve as a black inky fluid? Is this of any value to the fungus?

By what means are fungal spores scattered?

Do you know of any fur-bearing animals which eat mushrooms?

How does a puffball differ from a gill fungus?

Some "Earth stars" mature under the surface of the ground. How do they get out?

Where do truffles grow with respect to the substratum? How are truffles gathered?

What are "fairy rings"? How are they formed?

Where may you find large pore-fungi?

What does the commercial mushroom grower mean by the term "spawn"?

What poisonous mushroom is sometimes called, poison cup, or death angel?

Do you know of any animals that grow mushrooms for food?

What are phosphorescent fungi?

Does the lack of chlorophyll in a plant make it a fungus? Are bacteria fungi? They are not so classified in this text. Why?

A bacterium, a fungal spore, and a yeast cell may be of the same form, size and appearance, etc. Under what circumstance could you know which is which?

What group of fungi resemble certain red sea-weeds in the development of the spore fruit?

What does spraying plants with fungicides accomplish?

What is the meaning of the term *sclerotium* as applied to fungi?

Are any human ailments caused by pathogenic yeasts?

CHAPTER XVI

BRYOPHYTA

The next great group of plants above the algae and fungi in the evolution of the plant kingdom is the Bryophyta. The word means moss-like plants. The Bryophyta comprise those plants commonly known as liverworts and mosses. In these plants the haploid and diploid structures in the life cycle are always easily recognized as distinct individuals. The haploid individual is called the *gametophyte*, and the diploid, the *sporophyte*. The term gametophyte means gamete-bearing plant; the word sporophyte means spore-bearing plant. The gametophyte is the larger, self-nourishing and independent individual, which may live from year to year or indefinitely. The sporophyte lives largely as a parasite upon the gametophyte. Its function is to produce spores, after which it dies. The sporophyte lives but one season. A gametophyte may produce more than one sporophyte. In case the gametophyte lives two or more years, it may produce one or more sporophytes each year. The sporophytes dry up and disappear soon after spore production, leaving the gametophyte to continue life save in the case of annuals. The alternate succession of gametophyte and sporophyte in the complete life cycle has long been referred to as the *alternation of generations*.

Those Bryophyta known as liverworts belong to the class, *Hepaticae*. The mosses constitute the subdivision, *Musci*. We may follow the life history of one representative of each class, together with a brief description of a few others of common occurrence.

HEPATICAE (LIVERWORTS)

PORELLA

As an illustration of the life history of a typical liverwort, one of the larger leafy forms, Porella, may be chosen. The plant is found commonly on the shaded sides of tree trunks near the ground, where the moisture is more constant, and on rocks where similar conditions prevail. Some species are aquatic, at least for the larger part of the year, growing in cool, rapidly flowing water.

The Gametophyte.—The gametophyte of Porella is a leafy axis, branching monopodially (Fig. 311). With age the basal and older part

of the plant dies and decays, while growth may continue at the distal ends, or growing points, for a long time, or indefinitely. The gameto-

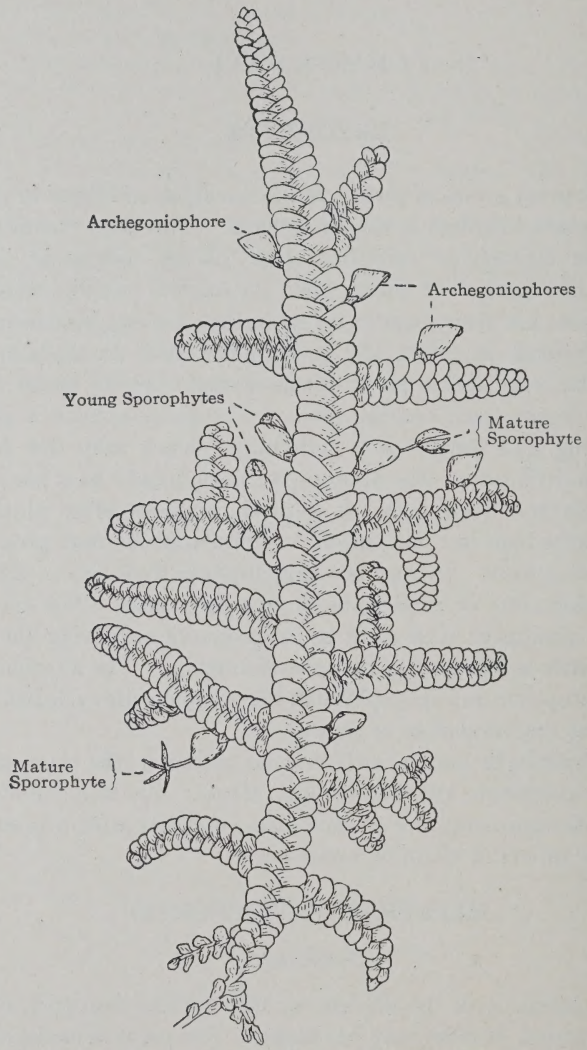


FIG. 311.—*Porella navicularis*. Part of a female gametophyte, seen from the dorsal side, showing arrangement of upper leaves, mode of branching, and several short, bud-like branches (archegoniophores), with sporophytes in different stages of development, and mature sporophytes with opened capsules.

phyte is dorsiventral; i.e., it has a distinct upper (dorsal) and under (ventral) side. The dorsal side is always turned toward the light, while the ventral side faces the substratum. The axis bears three rows of leaves,

two rows on the dorsal side, and one row on the ventral side. The upper leaves overlap like the shingles of a roof. On the ventral side of the axis is borne a single row of small leaves. The dorsal leaves are two-lobed, the smaller lobe being concealed by the upper when viewed from above. When the leaves are much crowded, as in the younger parts of the plant, the aspect of the under side is that of three rows of leaves. This is because the lower lobes of the dorsal leaves are of about the same size as the ventral leaves (Fig. 312 A).

Whitish rhizoids (brown in older parts) fasten the plant to the substratum. These are neither conspicuous nor abundant.

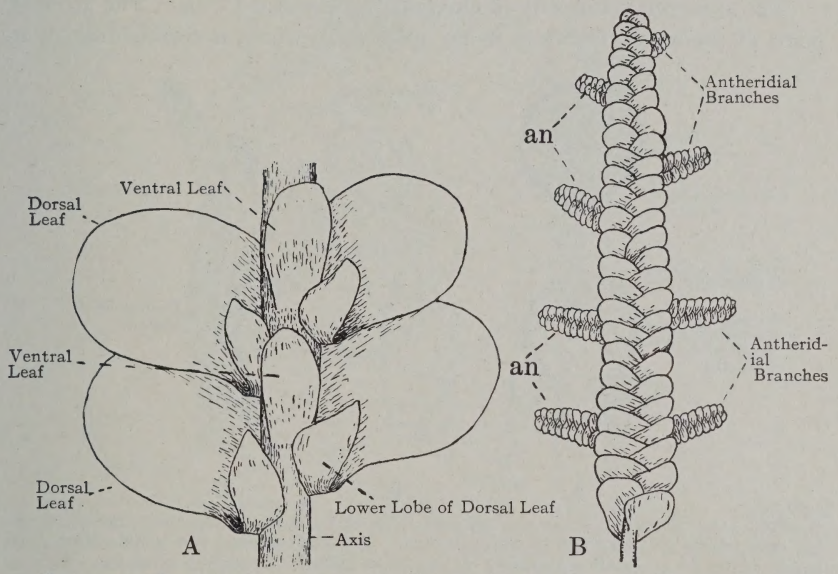


FIG. 312.—*Porella navicularis*. A, small part of gametophyte seen from the ventral side. B, dorsal view of branch of male gametophyte, showing antheridial branches, (antheridiophores) *an*.

Porella is dioecious. The female plants may be recognized by the presence of one or more small brownish structures, the mature *sporophytes* (Fig. 311), resembling tiny flowers, borne on small, dwarf, bud-like, branches. If such a *younger* bud be opened, the young sporophyte will be seen as a small green knob (Fig. 313, A). The male plants are recognized by their smaller lateral branches with smaller and more closely imbricated leaves (Fig. 312, B). These branches bear the antheridia.

The Sporophyte.—The sporophyte consists of a terminal, globular *sporangium*, or capsule, a *stalk*, or *seta*, and a *foot* (Fig. 313, B). The capsule opens by four valves, liberating two kinds of cells, globular *spores*, and long, tubular *elaters* (Fig. 313, C, D). Each spore has a firm cell wall,

provided externally with numerous very small conical thickenings somewhat hooked at the tip. The fresh spores reveal green chloroplasts. The elaters are slender, tubular cells, with two or more spiral thickenings on the inner surface. The mature elaters are devoid of living substance. In a comparatively short time after the sporangium opens the sporophyte dries out and falls away.

Structure of the Gametophyte.—The leaves of Porella are one cell thick, and without a midrib. Each cell is uninucleate, and possesses a number of chloroplasts. Sometimes cells are present containing chiefly a brown oily substance.

The axis consists mostly of elongated, thin-walled cells. The growing point of the axis terminates in an apical cell, which is tetrahedral, or in

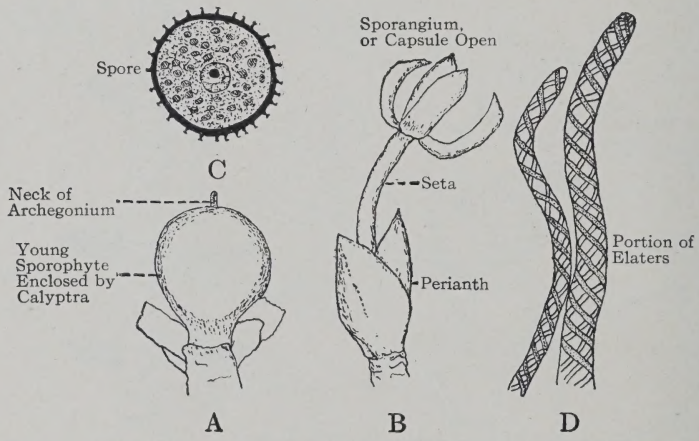


FIG. 313.—*Porella navicularis*. A, end of dwarf branch, with leaves removed, showing sporophyte still enclosed by the calyptra. B, fully matured sporophyte with open sporangium, from which spores and elaters have fallen. C, section of spore. D, portions of two elaters.

the form of a triangular pyramid, with the base representing the free outer surface. By division, cells are cut off from the three lateral surfaces. Two of the cutting surfaces of the apical cell face toward the dorsal side, while the third looks toward the ventral side of the gametophyte. Each cell thus cut off from the apical cell may give rise to a leaf, with the result that three rows of leaves are developed, two on the dorsal, and one on the ventral side.

Vegetative Propagation of the Gametophyte.—The older, or basal parts of the gametophyte die and decay, isolating the branches, which may continue to grow at the tip, thus becoming separate individuals.

The Antheridium.—The antheridia are borne in the axils, or slightly above the axils of the small, closely imbricated leaves of the special

branches mentioned above (Fig. 314, A). Each antheridium consists of a globular body and a short, slender stalk. The wall of the antheridium is three cells thick below, and one cell thick above. Within is a large number of very small cells, which give rise to the sperms. Each sperm is a cell so transformed as to be capable of locomotion in water (Fig. 314, C). It is a spirally twisted body bearing two cilia at the slender anterior end. The thicker posterior part consists largely of the condensed nucleus, while the anterior end is a very delicate thread, the *blepharoplast*, which bears the two long cilia. A vesicle may adhere to the posterior extremity.

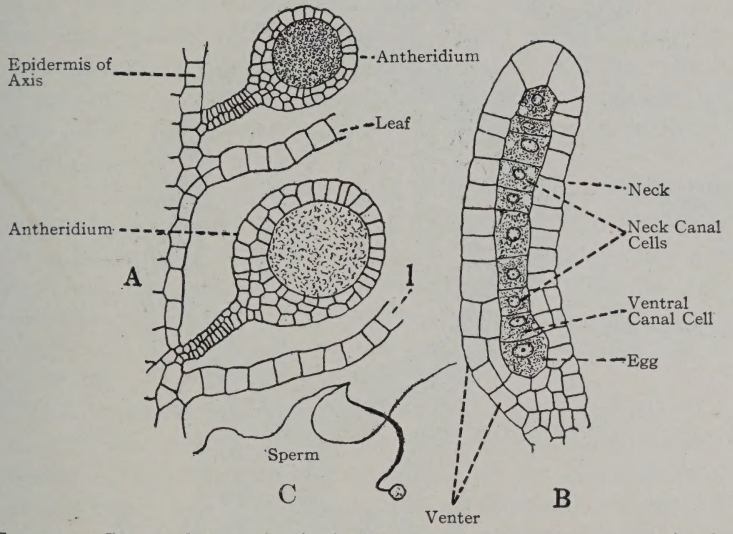


FIG. 314.—*Porella bolanderi*. Antheridium and archegonium. A, longitudinal section of two antheridia of different ages, showing manner of attachment to axis, only the epidermis of the axis being drawn. B, longitudinal section of archegonium. C, sperm. (A, from Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers. C, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

The Archegonium.—The oögonia, here designated as *archegonia*, are borne in terminal clusters on very short branches, which in younger parts of the plant are partly concealed by the dorsal leaves. On older parts such branches appear as small buds, as stated in the foregoing. The archegonium is a flask-shaped organ having a short stalk (Fig. 314, B). The lower, enlarged, part is the *venter;* the upper part is the *neck*. As will readily be seen the organ consists of an axial row of cells, shaded in the figure, surrounded by an outer layer of cells. The outer layer, or wall, of the neck is one cell thick, while that of the venter may be two cells in thickness. The lowermost cell of the axial row is the egg. The cell just above the egg is the ventral canal cell, and the others are the neck canal cells. The egg and ventral canal cell are sisters in origin.

The antheridia and the archegonia originate each in a single epidermal cell, but their development is too complicated to be discussed here.

The Process of Fecundation.—As the archegonium reaches maturity the neck canal and ventral canal cells are disorganized into a mucilaginous

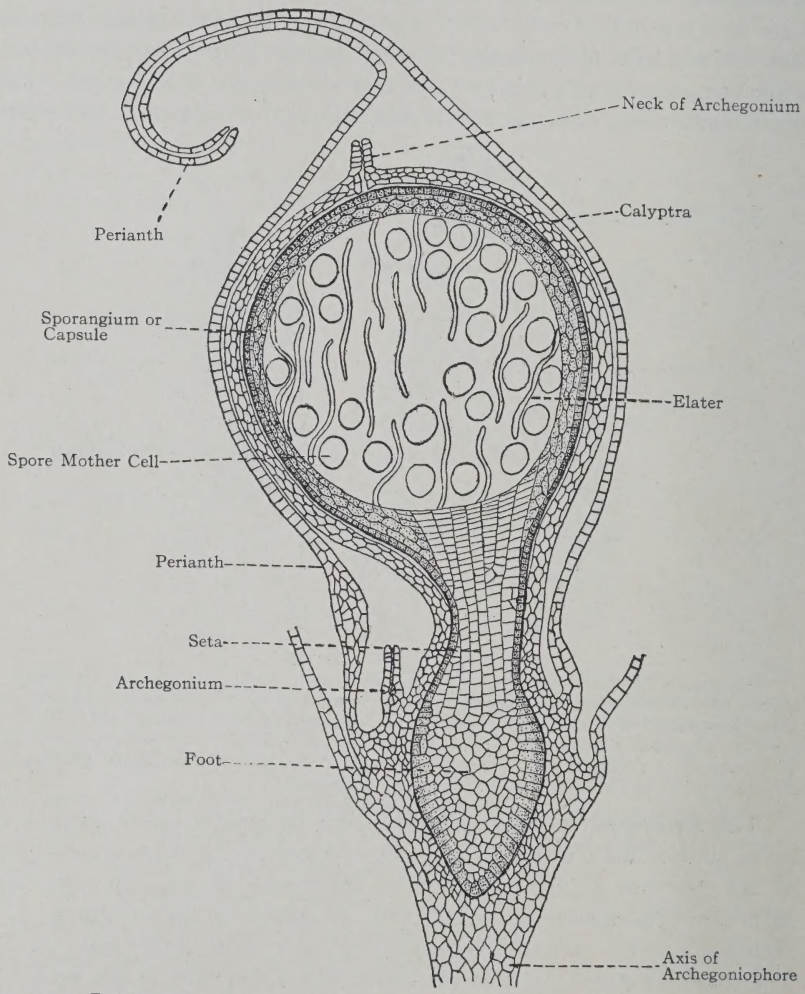


FIG. 315.—*Porella navicularis.* Longitudinal section through a dwarf branch (archegoniophore) with immature sporophyte enclosed within the calyptra.

substance. If water be now applied to the ripe archegonium, the neck will open at the top, and some of the mucilaginous material will be expelled and will begin to diffuse in the water. The egg remains in the venter.

As the antheridium ripens, the walls of the sperm-bearing cells likewise change into a mucilaginous substance. When wetted with water the ripe organ opens and the sperms are set free. They swim about actively in the water derived from rain or heavy dew in their native habitat. When the sperms are sufficiently near the opening of the neck of the archegonium, they enter and pass down to the egg. The entire sperm enters the cytoplasm of the egg, and finally its nucleus fuses with that of the egg. The fecundated egg, or zygote, now begins its development into the sporophyte. It is evident that the cells of the sporophyte will have the double number of chromosomes.

The Development of the Sporophyte.—Soon after fecundation the neck of the archegonium shrinks and turns brown, but the venter continues growth as a cover for the sporophyte. The sporophyte reaches maturity within the enlarged venter of the archegonium, which is now called the *calyptra.*

The form and general structure of the sporophyte, and its relation to the end of the axis bearing it, will be made clear in Fig. 315, which is a view of a longitudinal section. The nearly mature sporophyte is differentiated into three regions, namely, the rounded upper end, the *sporangium*, the constricted middle part, the *seta*, and the expanded lower end, the *foot.* The foot absorbs water and food from the axis of the gametophyte.

Within the sporangium two kinds of cells are differentiated, long, slender cells that develop into elaters, and globular spore mother-cells. The spore mother-cells soon become four-lobed and give rise each to a tetrad of spores. In the formation of the tetrad from the mother-cell, two nuclear divisions characteristic of spore mother-cells in the higher plants take place. The first of these mitoses is a reducing division by which the number of chromosomes is reduced one-half. The second is an equational division. Each spore possesses, therefore, the single (haploid) number of chromosomes. The spore is, then a one-celled gametophyte; all cells of the gametophyte, which come from the spore, contain the single number of chromosomes.

The sporophyte reaches maturity within the calyptra. The seta then elongates, and the sporangium is forced out through the ruptured wall of the calyptra and beyond the enveloping leaves of the bud. The capsule opens by four valves, and spores and elaters are set free. As the elaters dry, they twist and become entangled in masses of varying sizes. In each tangle of elaters may be held several to many spores. The spores and elaters are scattered chiefly by the wind. When the mass strikes a moist surface, the elaters straighten out and free the spores, which may adhere to the substratum. The elaters are effective in the deposition of

spores in groups. Since about one half of the spores are potentially male, and the other half potentially female, gametophytes of both sexes are enabled to develop together on a very small area.

Summary of the Life History of Porella.—From the foregoing we have learned that the sporophyte is derived from the union of egg and sperm. It reaches maturity within the calyptra, deriving nearly all of its nourishment from the gametophyte. The sporophyte lives, therefore,

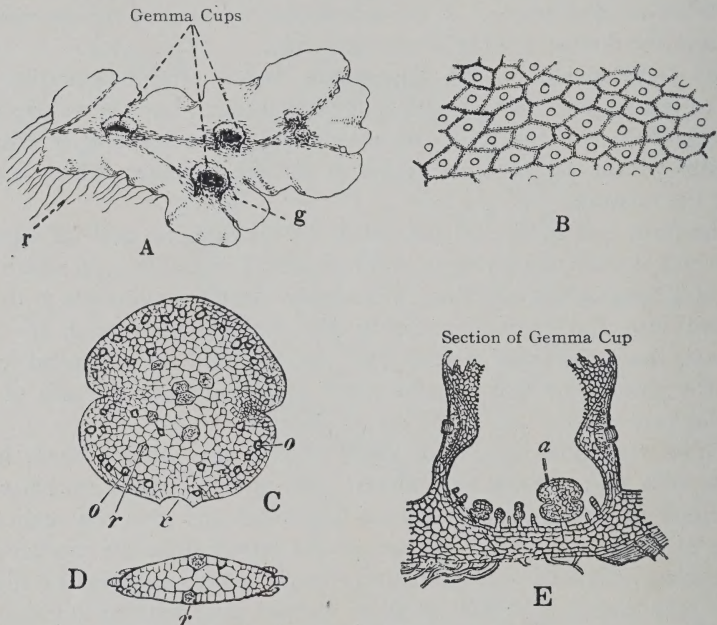


FIG. 316.—*Marchantia polymorpha*. A, portion of gametophyte with gemma cups, *g*: *r*, rhizoids. B, several rhombic areas of the dorsal surface of the thallus. C, a gemma; *o*, oil-bearing cell; *r*, rhizoid initial cell; *x*, place of attachment. D, vertical section of gemma, showing growing point at left and one at right. E, diagram of vertical section of gemma cup, showing manner in which gemmae are borne; *a*, gemma.

as a parasite on the gametophyte. After the spores are developed the sporophyte dies. Spores grow into gametophytes, and these bear the gametes. One step in the life-history is aquatic.

Diagram of the life cycle of the liverwort:

Gametophyte (haploid) ⟨ antheridium—sperm / archegonium——egg ⟩ zygote (diploid) → sporophyte (diploid) →

spore (diploid) mother-cells → reduction division → spores (haploid) → gametophyte. (haploid)

MARCHANTIA

As a representative of a liverwort in which the gametophyte is a flat, ribbon-like *thallus*, we shall select the well known and beautiful *Marchantia polymorpha*. It may be found in moist, shady places on the ground, not infrequently near the foundation on the shaded sides and walls of buildings. In cultivation it grows well on coal ashes or on earth.

The Gametophyte.—The gametophyte has the form of a flat, ribbon-like, fleshy, deep green, dorsiventral thallus, which branches dichotomously. Each branch is traversed by an inconspicuous midrib, which leads to a growing point located in a notch or depression at the distal end of the branch (Fig. 316, A). The upper, or dorsal surface is marked by polygonal areas generally rhombic in outline (B). Near the center of each area is a stoma leading to a cavity beneath the epidermis. Each cavity is as large as the rhombic area, and is separated from similar neighboring cavities by partitions generally one cell in thickness. These partitions beneath the epidermis correspond to the boundaries of the areas as seen externally. Along the margin in fresh and rapidly growing plants may be seen a row of small pinkish scales.

From the lower epidermis of the thallus are developed numerous unicellular rhizoids, which fasten the plant to the substratum and absorb water (*r*). The rhizoids are of two kinds: those springing from the midrib are large and smooth-walled (Fig. 317, B); those arising on either side of the midrib are smaller and have undulating walls with peg-like thickenings projecting into the cavity of the cell. In some rhizoids the thickenings are small and conical; in others they are large and irregular in shape (C, D).

Along the midrib on the under side are also two rows of minute scale leaves that originate at the growing point (Fig. 317). These are not readily seen even with the aid of a pocket lens. They serve to protect the tender cells of the growing point from too rapid desiccation, and probably from mechanical injury. On the younger scale leaves overlapping the growing point are glandular hairs which secrete a mucilaginous substance.

Vegetative Propagation.—The gametophyte of Marchantia propagates vegetatively in two ways: by the death and gradual decay of older parts, by which branches are disconnected; and by means of specialized shoots known as *gemmae*. The gemmae are borne in small cups on the dorsal surface (Fig. 316, A, *g*). Each gemma is a flat, rounded structure with a basal scar indicating the place of attachment to the short stalk on which it was borne, and with two notches indicating the growing points (C, D).

From the bottom of the cup spring also short glandular hairs which secrete a mucilage. By the swelling of this mucilage, and by the growth of young gemmae beneath, the mature gemmae are detached (E). Eventually they are scattered by rain, and in favorable localities begin to grow in two directions into new plants. Both sides of the gemma are alike, and that which happens to be next to the substratum becomes the ventral, and the other the dorsal, side of the thallus. Gemmae are produced in great numbers during the earlier vigorous vegetative period of growth, before the appearance of the sex organs.

Structure of the Thallus.—The details of structure of the adult thallus may be readily understood from a transverse vertical section (Fig. 317, A). Along the dorsal side are the large air-chambers roofed over by the epidermis. From the floor of each air chamber arise cactus-like

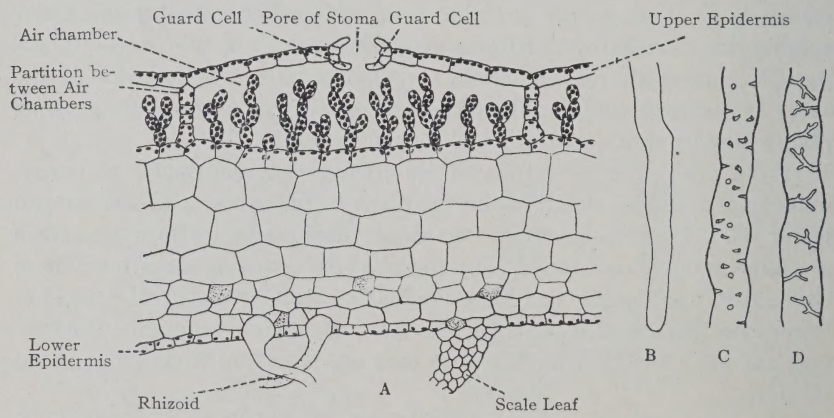


FIG. 317.—*Marchantia polymorpha.* Structure of the thallus. A, vertical section showing one large air-cavity beneath the epidermis. B, C, D, portions of each of three kinds of rhizoids, the last two with inner thickenings of the wall.

clusters of thin-walled cells containing many large chloroplasts (A). These cells constitute the principal photosynthetic tissue of the plant, although a few smaller chloroplasts are present in the epidermis and in other parts of the thallus. The pore is surrounded by a structure resembling a chimney, or a barrel with the ends removed. This structure consists generally of four tiers of cells, each tier being made up of four cells forming a ring. The four cells of the inner tier are larger, and constitute the guard cells, which tend to open and close the pore.

The tissue below the layer of air chambers is composed of large and nearly colorless cells. Here and there among these may be found certain cells filled with mucilage, while others contain an oily substance. The epidermis on the under side is made up of smaller cells with few chloro-

plasts. From the epidermal layer near the growing point the rhizoids and scale leaves arise.

The Growing Point.—The growing point terminates in one or more initial cells known as apical cells, from which all parts of the plant are primarily derived. Each apical cell is wedge-shaped, and divides by cutting off new cells alternately from the dorsal and ventral faces.

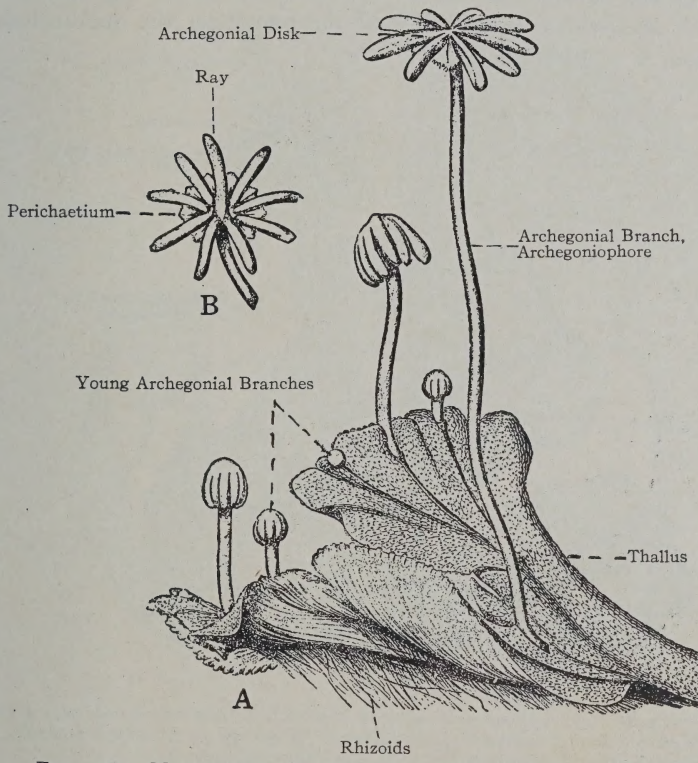


FIG. 318.—*Marchantia polymorpha*. A, portion of female gametophyte with archegoniophores in different stages of development. (Courtesy of Standard Scientific Corp., formerly Scientific Equipment Dept. of Kny-Scheerer Corp.)

The Sex Organs.—Marchantia is dioecious, but male and female plants cannot be distinguished as such before the appearance of the specialized branches that bear the sex organs. The archegoniophore consists of a slender, upright stalk bearing a conspicuous terminal star-shaped structure or disk (Fig. 318, A). The antheridiophore has a similar stalk, bearing at its upper end a circular disk with a lobed margin (Fig. 319). The structure of both the archegoniophore and the antheridiophore is similar to that of corresponding parts of the flat thallus.

The archegonia originate in the notches between the rays of the star-shaped structure, just back of the growing points. They appear to be on the lower side, but arise really on the morphological upper side, which becomes turned under by the peculiar growth of the disk (Fig. 320).

The archegonium is similar to that of Porella, namely, flasked-shaped, and consisting of a central row of cells surrounded by a wall one row of cells in thickness. The lowest cell of the central row is the egg, the one next above it the ventral canal cell, and the remainder the neck canal cells (Fig. 320, A, *a*, B).

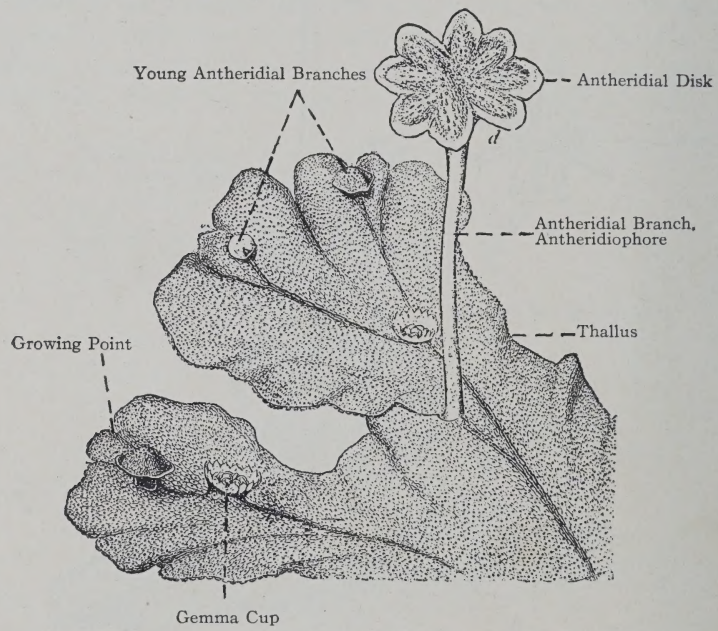


FIG. 319.—A portion of male gametophyte of Marchantia bearing gemma cups and antheridiophores in different stages of development. (Courtesy of Standard Scientific Corp., formerly Scientific Equipment Dept. of Kny-Scheerer Corp.)

The antheridia are located in flask-shaped cavities in the upper surface of the antheridial disk (Fig. 321, A, *a*, *c*, *d*, *e*, *f*). Each is a slightly elongated body with a short stalk (Fig. 321, B). The wall consists of a single layer of cells. Each small cubical cell within the body of the antheridium gives rise to two sperms after undergoing a diagonal division. The sperm is similar in structure to that of Porella.

Fecundation and Development of Sporophyte.—When the sex organs are ripe they open on the application of water. The sperms ooze out on the surface of the antheridial disk in small drops of mucilaginous substance and are scattered by raindrops. If the water containing sperms

falls on an unexpanded archegonial disk (Fig. 318, A) it will flow down between the rays and be drawn by capillarity to the archegonia, bringing the sperms to the open necks. The mucilaginous substance derived from the neck canal cells exerts a chemotactic stimulus upon the sperms, and they enter the archegonia, and one finally unites with the egg (Fig. 320, A, B).

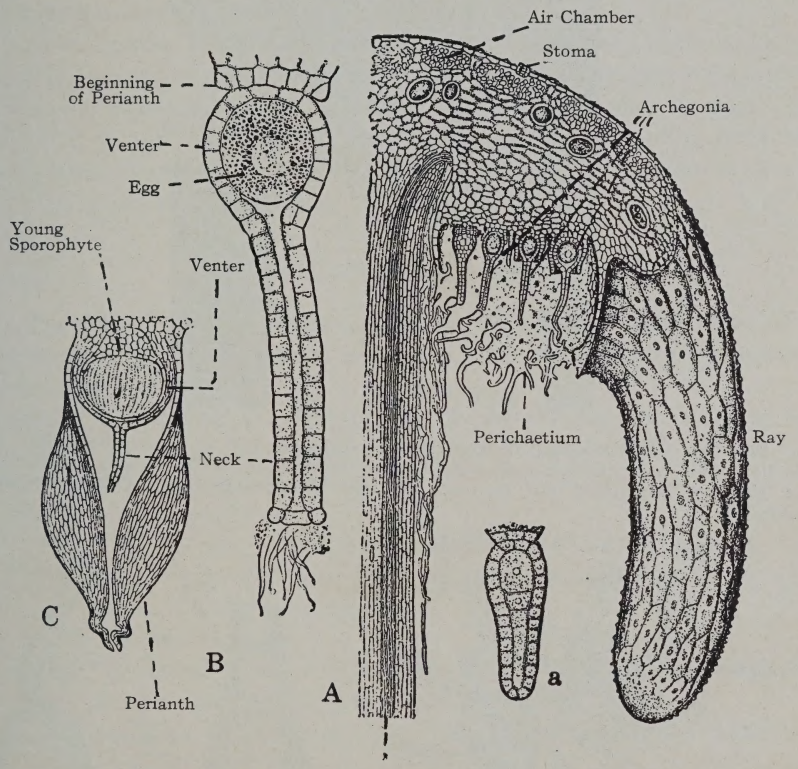


FIG. 320.—Marchantia. A, one-half of vertical section of archegoniophore, showing four archegonia in position; *a*, section of young archegonium. B, section of open archegonium with egg ready for fecundation and sperms at entrance of neck. C, section of young sporophyte inside calyptra. (Courtesy of Standard Scientific Corp., formerly Scientific Equipment Dept. of Kny-Scheerer Corp.)

The fertilized egg, or zygote, immediately begins to develop into the sporophyte. The younger stages of the sporophyte are spoken of as the embryo. The embryo is globular at first, but later becomes pear-shaped (Fig. 320, C). The sporophyte reaches maturity within the venter of the archegonium, which keeps pace with the growth of the former and becomes the *calyptra* as in Porella. In the nearly mature sporophyte three parts are recognized: the rounded *capsule*, the stalk or *seta* and the

foot, which fastens the sporophyte to the tissue of the gametophyte and absorbs food and moisture from it.

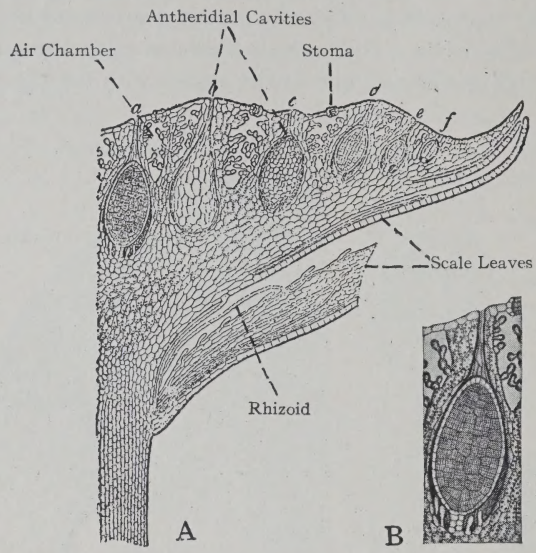


FIG. 321.—Marchantia. A, vertical section of one-half of antheridial disk. B, section of an antheridium in antheridial cavity, showing surrounding tissue. (Courtesy of Standard Scientific Corp., formerly Scientific Equipment Dept. of Kny-Scheerer Corp.)

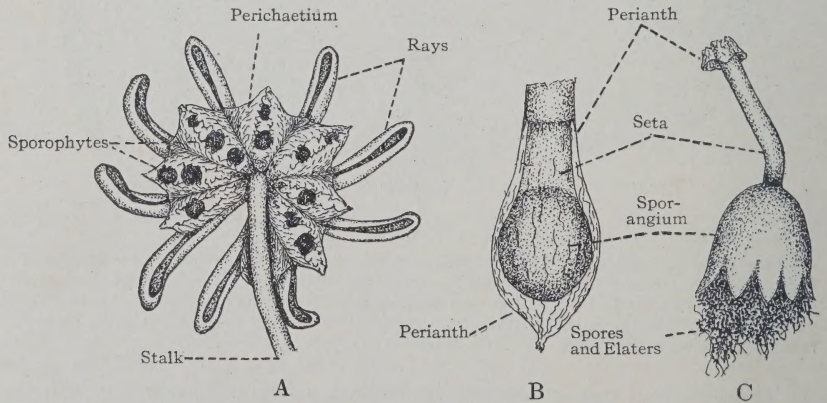


FIG. 322.—*Marchantia polymorpha*. A, underside of archegoniophore, showing sporophytes in position. B, mature but unopened sporophyte within the perianth. C, opened mature sporophyte, spores and elaters escaping.

During the development of the sporophyte there grows up around the archegonium, from its base, an enveloping membrane one cell in thickness. This envelope has been called the *perianth*, or *pseudo-perianth* (Fig. 320, C, Fig. 322, B). The membrane surrounding the group of sporophytes

developed between any two finger-like rays of the archegonial disk is called the *perichaetium* (Fig. 322, A, and Fig. 320, A). It has a fringed or lacerated edge.

Morphologically the archegonial disk represents a set of branches, the spaces between the rays representing the midribs. Each midrib, except the one representing the stalk of the archegoniophore, bears a row of archegonia surrounded by a perichaetium.

As in Porella, two sorts of cells are ultimately formed in the capsule, namely, spores and elaters (Fig. 322, C). When the sporophyte is mature the stalk elongates greatly, forcing the sporangium out through the ruptured calyptra and beyond the opening of the surrounding perianth and perichaetium (Fig. 322, A, C). The sporangium or capsule now opens and the spores are dispersed by the wind.

Classification of Liverworts

The known species of liverworts may be grouped under two subclasses, the Hepaticae, typical liverworts, and the Anthocerotae, horned liverworts.

Subclass I. Hepaticae.—The typical liverworts may be included in the following orders and families. Under each family will be given some of the genera commonly met with.

Ord. 1. Marchantiales.

Fam. Ricciaceae.—Sporophyte consisting of only a capsule. A rudimentary foot may be recognized in early stages of certain forms. No elaters are present.

Riccia, Ricciocarpus

Fam. Marchantiaceae.—Sporophyte with a stalk and a capsule of about equal length. Elaters are present.

Marchantia, Lunularia, Reboulia, Conocephalus (Fegatella), Fimbriaria

Ord. 2. Jungermanniales.

Fam. Jungermanniaceae.—Sporophyte with stalk three or more times the length of the capsule. Elaters present.

Thallose forms (Anacrogynae) Pellia, Aneura, Metzgeria, Pallavacinia

Foliose forms (Acrogynae) Porella, Frullania, Lejeunia

Subclass II. Anthocerotae.—The Anthocerotae, or horned liverworts, differ so fundamentally from the rest of the liverworts that the author has followed the suggestion of Campbell and has placed these plants in a separate class. In the deep-seated archegonia and antheridia, and in the early development of the sporophyte these plants resemble such lower

ferns as Ophioglossum and Botrychium. A further diagnosis is given in a subsequent paragraph.

ORD. Anthocerotales.

Fam. Anthocerotaceae.—Anthoceros, Notothylus, Dendroceros

RICCIACEAE

The genera Riccia and Ricciocarpus are commonly spoken of as the mud-flat liverworts because of their occurrence on muddy flats, on the

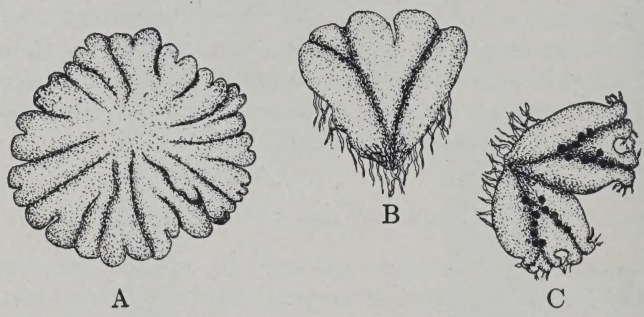


FIG. 323.—Riccia and Ricciocarpus. A, habit of *Riccia frostii* Aust. B, C, floating form of *Ricciocarpus natans*, the latter (C) bearing a row of sporophytes along each midrib.

firm, moist banks of streams, and in similar localities. Some species, as *Ricciocarpus natans*, grow as floating aquatics, as well as on the ground.

The gametophyte is a dichotomously branched, dorsiventral thallus, frequently forming circular, rosette-like expansions a centimeter or more in diameter (Fig. 323, A). A single row of scales developing on the lower side of the thallus later split in the middle to form two rows. Rhizoids are developed in the terrestrial forms but not in the floating forms. The midrib and ventral region are composed of closely arranged cells, while the dorsal region is usually very loose and spongy, owing to the presence of numerous intercellular spaces of varying size, many of them becoming large air chambers. Many of these air spaces are in communication with the outer air by means of pores in the epidermis.

The antheridia and archegonia are embedded in the tissue of the midrib on the dorsal side, being developed from superficial cells just back of the growing point.

The sporophyte, which is also embedded in the tissue, consists of merely a capsule, or a capsule and a poorly developed foot (Fig. 324). No elaters are present. The spores are set free after the thallus dies and decays. As stated in a preceding paragraph, species of Ricciocarpus live as terrestrial forms and as floating aquatics. On solid earth the rosettes are larger and characteristically smooth and trim in appearance, while

as a floating aquatic no rhizoids are developed, but numerous scales on the ventral side become very large and conspicuous (Fig. 323, B, C).

MARCHANTIACEAE

In addition to the well-known Marchantia, the genera Conocephalus (Fegatella), Reboulia, Fimbriaria, and Lunularia are commonly met with.

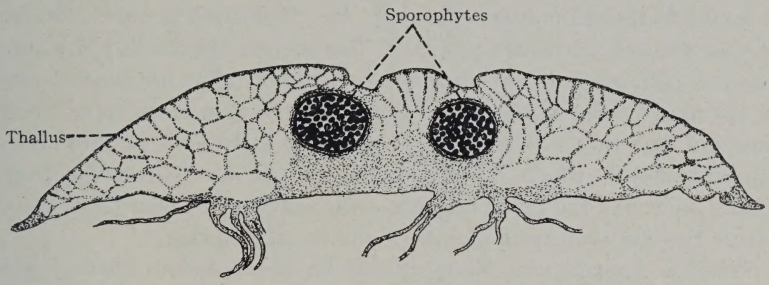


FIG. 324.—*Ricciocarpus natans*. Diagram of cross section of thallus, showing sporophytes embedded in midrib.

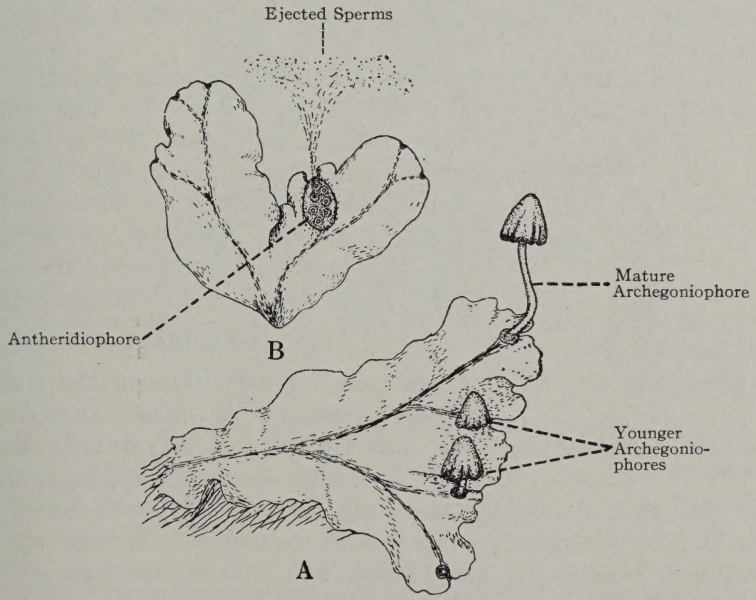


FIG. 325.—*Conocephalus conicus* (*Fegatella conica*). A, portion of gametophyte with archegoniophores bearing sporophytes. B, portion of gametophyte with a sessile antheridiophore from which sperms are being forcibly discharged.

Conocephalus conicus Dum. (*Fegatella conica* Corda.) is probably the largest of our liverworts. It grows abundantly on moist, shady earth, and especially on limestone ledges that are quite moist for a large part

of the year. The gametophyte resembles that of Marchantia with the exception that the rhombic areas on the dorsal surface are larger and more conspicuous. The plant gives off a characteristic odor. The antheridiophore is sessile, resembling a wart-like structure just back of the growing point (Fig. 325, B). The archegonial disk is conical, without the finger-like rays as is Marchantia, and it is mounted on a long slender stalk when the sporophytes are mature (Fig. 325, A). The stalk is very short until the sporophytes are nearly mature. The sperms are forcibly discharged from the antheridium. In greenhouse cultures, if the antheridial plants are sprinkled with water, especially after their surfaces have become somewhat dry, tiny volleys of mist containing sperms will be shot up from antheridiophores, which mushroom out in still air like smoke from a volcano, and may fall on archegonial disks that may be near (Fig. 325, B). Mature fruiting specimens may be found in early spring.

Reboulia hemispherica Raddi (*Asterella hemispherica* Beauv.) grows on earth and limestone in relatively dry places. The ventral surface is purple with a row of scales on each side of the midrib. The archegonial disk is conic-hemispheric, becoming flattened above, and usually four-lobed.

Fimbriaria tenella Nees resembles Reboulia in some respects. The gametophyte has the midrib thickened into a keel. The two rows of scales beneath are purple. The archegonial disk is conic or hemispheric, bearing usually four sporophytes, which are surrounded by a fringed envelope. The plant is monoecious. Lunularia is chiefly a greenhouse form, recognized by the crescent-shaped gemma cups.

FIG. 326.—*Pellia epiphylla.* Gametophyte bearing mature sporophyte.

JUNGERMANNIACEAE

In such representatives of the thallose Jungermanniaceae as Pellia, Aneura, etc. the gametophyte is a flat, dorsiventral thallus, smaller and much simpler in structure than that of the Marchantiaceae. In *Pellia epiphylla* Raddi, for example, the sex organs are immersed in the thallus. When mature, the sporophyte consists of a long colorless seta, with the terminal, globular capsule opening by valves (Fig. 326).

The leafy Jungermanniaceae are typified by Porella, which is, however, a relatively large form. Frullania, Lejeunia, etc. are relatively small and inconspicuous, growing on logs and tree trunks. A species of Porella found in Indiana is aquatic. It grows attached to limestone in cool, rapidly flowing water.

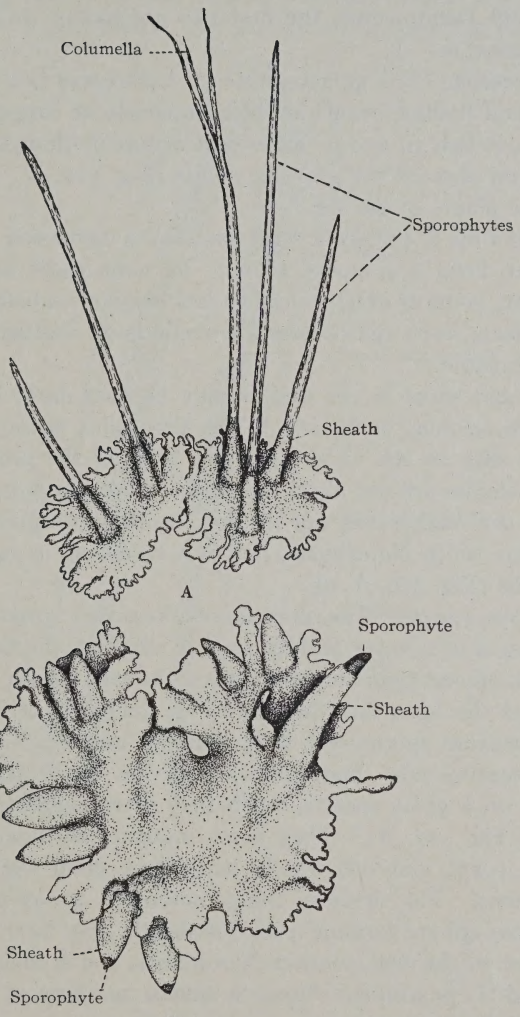


FIG. 327.—*Anthoceros punctatus* and *Notothylas orbicularis*. A, gametophyte of *A. punctatus* bearing several sporophytes in different stages of development, the oldest one, having opened by a longitudinal slit, shows the columella between the two halves; ×6. B, gametophyte of *N. orbicularis*, with several almost horizontal sporophytes. ×10.

ANTHOCEROTACEAE

Of the three genera of the Anthocerotaceae, namely, Anthoceros, Notothylas, and Dendroceros, the first two are native to our flora, and the third is tropical.

Anthoceros.—The gametophyte of Anthoceros is a small, dark green, dorsiventral thallus, branching dichotomously or irregularly and forming rosettes one-half to one or more centimeters in diameter. The irregular edges often obscure the growing points (Fig. 327, A). Delicate rhizoids fasten the plants to the soil.

The thallus is simple in structure, being composed of rather uniform cells that form a compact tissue. In some cases intercellular spaces are present, some of which contain a mucilaginous substance. Except in a tropical form, each cell possesses a single large characteristic chloroplast with a pyrenoid.

Here and there in the thallus may be seen dark, blue-green specks, which are colonies of Nostoc. The alga gains entrance through small mucilage slits on the under side just back of the growing point. The Nostoc colonies are not always present. They do not seem to be of any value to the Anthoceros, nor do they cause any injury. The growth of the thallus, as in Notothylas, proceeds from one or more wedge-shaped apical cells (Fig. 329, A, *a*).

The Sporophyte.—The sporophyte differs very greatly from that of any other class of liverworts, and, because of this fact, the Anthocerotaceae are of special interest from the standpoint of the evolution of the liverworts, and because of the light that they throw on the origin of the lower ferns.

The mature sporophyte is cylindrical, and may attain a length of several centimeters. Sporophytes may be developed in considerable numbers on a given rosette, when they often suggest a very small tuft of grass (Fig. 327, A). They reach maturity outside the venter, being green in color, and not wholly dependent upon the gametophyte for nourishment. The tissue of the gametophyte grows up about the base of each sporophyte forming a sort of sheath (Fig. 327). The cells of the outer part, or the wall, contain chloroplasts, one in each cell in *Anthoceros laevis* and *A. punctatus*. Stomata similar to those of higher plants are present in the epidermis.

The sporophyte does not, as in other liverworts, consist of a seta and capsule, in which the spores all mature at the same time. On the contrary, the spores mature a few at a time, but continuously throughout the life of the sporophyte.

The structural plan of the sporophyte is illustrated in Fig. 328, which is a diagram of a longitudinal section. The lower end consists of the bul-

bous foot, which is embedded in the tissue of the gametophyte. Extending up through the center is the columella. Surrounding the columella is the spore-bearing region, several cells in thickness, which extends over the upper end of the columella. The meristematic region is just above

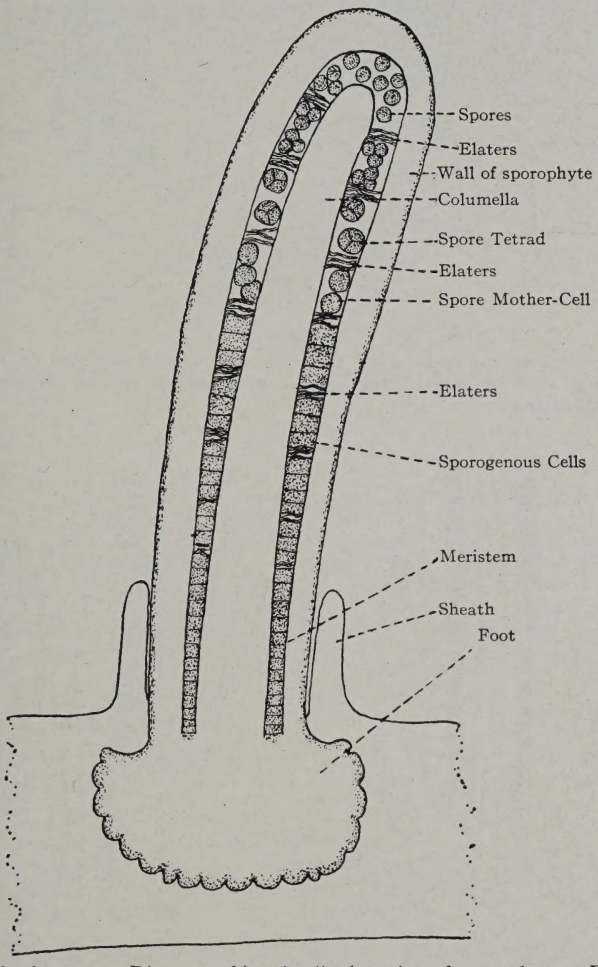


FIG. 328.—Anthoceros. Diagram of longitudinal section of sporophyte. Explanation in text.

the foot. The wall of the sporophyte is several cells in thickness. In the spore-bearing region, from the growing zone upwards, smaller sterile cells, which will give rise to elaters, alternate with larger cells that will produce the spores. Beginning with the tip of the sporophyte, we find first mature spores followed downwards by spore tetrads, both being

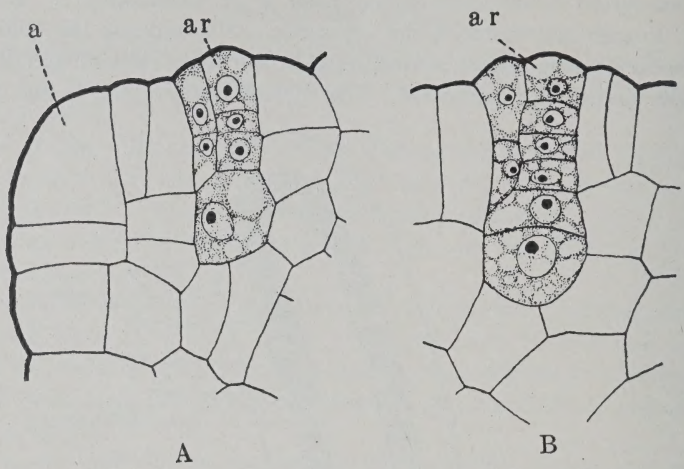


FIG. 329.—*Notothylas orbicularis*. Growing point and archegonia. A, longitudinal section through growing point of thallus. B, archegonium almost mature. *a*, apical cell; *ar*, archegonium.

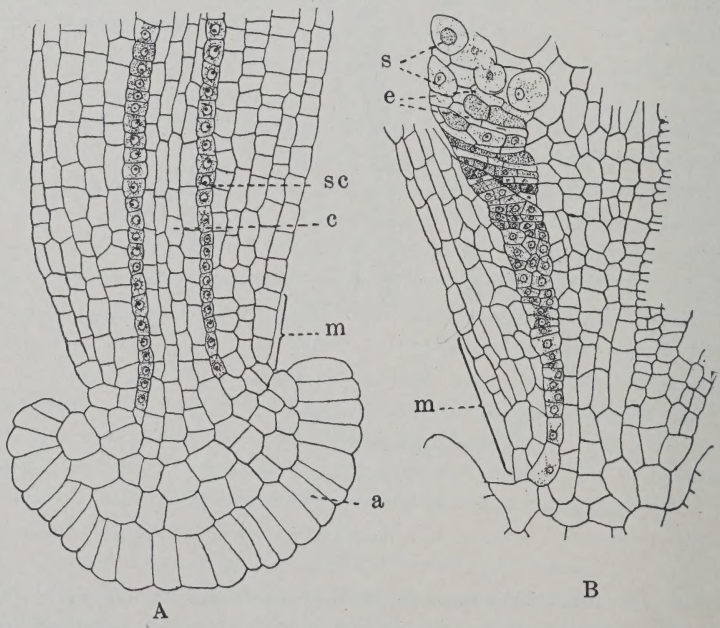


FIG. 330.—Notothylas. A, longitudinal section through base of young sporophyte. B, longitudinal section of one half of base of older sporophyte. *a*, foot; *m*, meristematic region at base of sporophyte; *c*, columella; *sc*, sporogenous tissue; *s*, spore mother-cells; *e*, elaters. (After Mottier.)

interspersed with the rudimentary elaters; below the tetrads come the spore mother-cells, and below these, alternating layers of spore-bearing and sterile cells. The structure of the lower part of the sporophyte is accurately shown in Fig. 330, A and B, which pertains to Notothylas, whose sporophyte is similar to that of Anthoceros. In Fig. 330, A, we have the large bulbous foot (*a*), with the outer layer of cells somewhat elongated. Above the foot is the meristematic zone (*m*), showing differ-

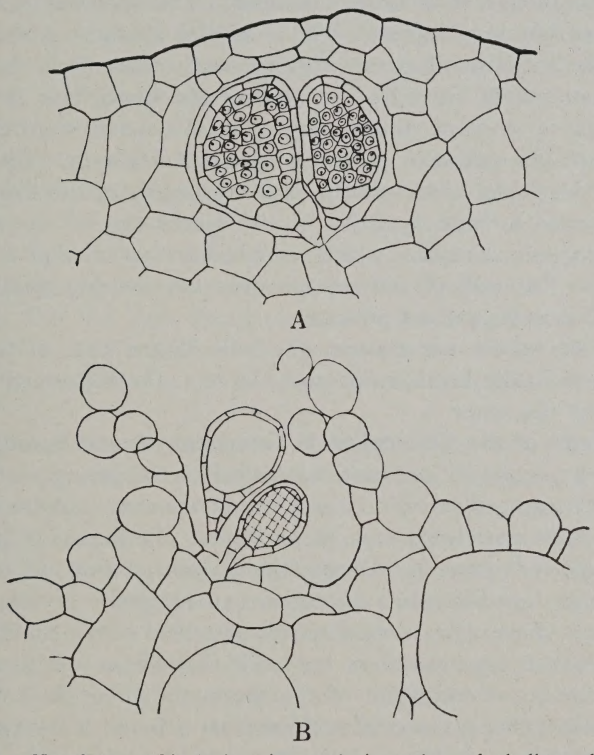


FIG. 331.—*Notothylas orbicularis*. A, vertical section of thallus, showing two antheridia in closed cavity beneath upper surface of gametophyte. B, section showing manner of opening of antheridial cavity.

entiation of spore-bearing cells (*sc*), and the columella (*c*) in the center. Fig. 330, B is a median longitudinal section of a part of the base of an older sporophyte, in which the successive layers of the sterile and spore-bearing cells are accurately shown, together with their origin in the meristematic region. The sporophyte of Anthoceros continues growth and spore production until the death of the part of the gametophyte that produced it, or until cold weather brings the life of the plant to an end.

The Sex Organs.—The antheridia and archegonia of Anthoceros and Notothylas are quite similar in structure and development. The antheridia arise in closed cavities beneath the epidermis (Fig. 331). The archegonium arises from a surface cell, but the mature organ is embedded in the tissue. The terminal cells of the neck may, however, project above the surface (Fig. 329, A, B).

Notothylas.—The gametophyte of Notothylas resembles that of Anthoceros, though it is usually smaller. The sporophyte is smaller, and it does not grow upright into a slender thread. After breaking through the calyptra, it curves forward and comes to lie horizontally on the thallus (Fig. 327, B). In general the sporophyte is similar in development to that of Anthoceros. The meristematic growth at the base is much less extensive, however, than in Anthoceros. Although the spores are developed first at the tip of the sporophyte, this structure does not open until a large majority of the spores are mature. There is formed, therefore, a capsule which resembles somewhat that of the other liverworts. The wall of the capsule does not develop photosynthetic tissue, and stomata are not present.

When the spores are mature, the cells at the base of the capsule elongate and finally break away from the foot, thereby severing all connection with the latter.

Continuity of the Chloroplast in Gametophyte and Sporophyte.—In a preceding paragraph attention was called to the presence of one large and characteristic chloroplast in each cell of the gametophyte and sporophyte of *Anthoceros laevis* and *A. punctatus*. In the spore mother-cell one chloroplast is present. During the division of this cell to give rise to the tetrad, the chloroplast undergoes two successive divisions, as does the nucleus. Each spore is consequently provided with a chloroplast, and this condition is maintained in each cell throughout the gametophyte. However, in the development of the sperm the chloroplast disappears, with the result that no trace of a chloroplast is found in connection with the mature sperm. In the egg, on the contrary, a chloroplast is present, though somewhat reduced in size, and from this the chloroplast of the sporophyte is derived. In other words, the sporophyte inherits its chloroplast through the egg alone.

Evolution of the Sporophyte in Liverworts.—When the structure and development of the sporophyte of the liverworts are taken into consideration, one finds a very noticeable series of progressive changes from the Ricciaceae to the Jungermanniaceae. In the Ricciaceae, which have the simplest sporophyte, this structure consists of but a sporangium or capsule. Foot and seta are lacking, or the former may be present in a rudimentary state. The first step in progress above this simple sporophyte is seen in

Marchantia, in which about one-half of the sporophyte (the distal half) becomes the capsule, the other half giving rise to the foot and the seta. One-half of the sporophyte has become vegetative (sterile) tissue. In the Jungermanniaceae progressive sterilization has proceeded much farther, about two-thirds to three-fourths being vegetative tissue. In these three families the sporophyte is almost wholly dependent upon the gametophyte.

When we come to the Anthocerotae, we find that progressive differentiation has gone much farther. There is first the large foot, then the meristematic region just above it, by which the mass of the sporophyte is increased, and finally the presence of a central strand of vegetative tissue, the columella. Added to these features we have the development of photosynthetic tissue, which is a long step toward the independence of the sporophyte. Further evidence of continued growth and greater independence of the sporophyte has recently been brought to light in a Californian species, *Anthoceros fusiformis* Aust., in which the sporophyte may attain a length of 16 centimeters. In this species the foot has been found to have become exposed, owing to the disintegration of the cells of the gametophyte. Under such circumstances it is possible that the foot may be able to absorb water from the soil.

In the liverworts the capsule of *Notothylas orbicularis* is intermediate between the type of the ordinary liverworts, the Hepaticae, and the more highly specialized spore-producing portion of Anthoceros. The sporogenous region in Anthoceros, with its alternating sections of spore-bearing and sterile cells, finds a striking parallel in the sporophore of Ophioglossum, one of the lower ferns (p. 366), in which the embedded sporangia alternate in a longitudinal series with vegetative tissue. In Ophioglossum the spores are set free through a lateral slit in each spore-bearing mass (sporangium), while in Anthoceros such is not the case. If, in Anthoceros, each spore-bearing aggregate of cells, separated by the sterile or elater-producing cells, were to open laterally by a slit to the exterior, and if the columella were to develop vascular tissue, the similarity between the sporophore of Ophioglossum and that part of the Anthoceros sporophyte above the meristematic zone would be complete.

Moreover, the embryo sporophyte of the Ophioglossaceae, with its large foot, bears a resemblance to the embryo of Anthoceros. If the meristematic zone of Anthoceros could be conceived as developing a root and a rudimentary leaf, we should then have a fern sporophyte. It is not difficult to imagine how the fern sporophyte, as it occurs in Ophioglossum, could have been derived from some ancestral form resembling the sporophyte of Anthoceros.

MUSCI (MOSSES)

The mosses are much more abundant than the liverworts, and in certain localities constitute a very characteristic feature of the vegetation.

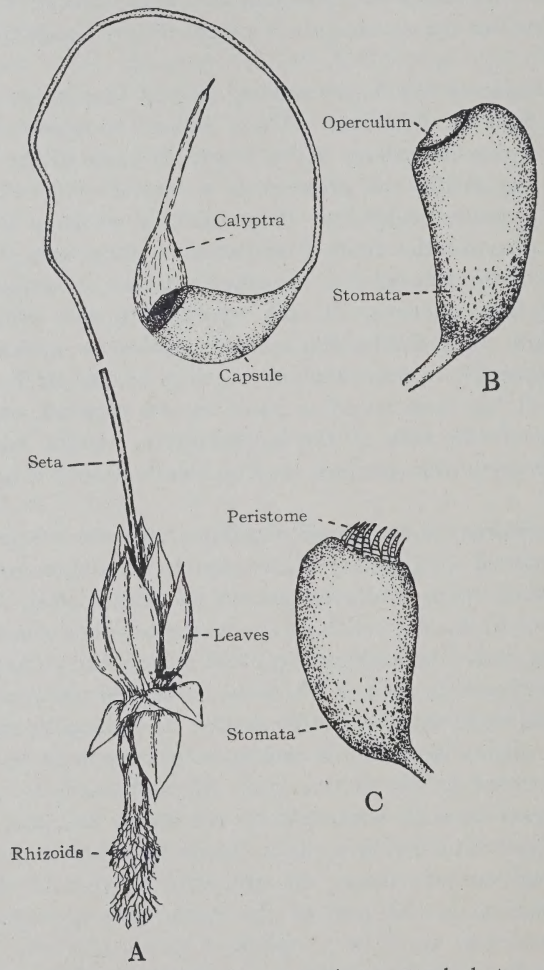


FIG. 332.—*Funaria hygrometrica*. A, sporophyte attached to gametophyte. B, capsule of sporophyte. C, ripe capsule after the operculum has fallen off.

The number of species is far greater than in the liverworts, but there is in general a greater uniformity in form and structure in the numerous species.

In general, a moss gametophyte may be distinguished from that of a leafy liverwort in that the former consists of an upright leafy axis or axes

whose spirally arranged leaves have a midrib. In some species the plants grow prostrate on the substratum and may present the appearance of dorsiventrality. The rhizoids are multicellular, consisting of branched filaments, usually with golden brown cell walls. The transverse walls of the rhizoids may be oblique.

The sporophyte, borne at the upper end of a leafy axis, is larger and more highly differentiated than that of the liverworts. It consists of a long slender *seta*, bearing at the distal end a large capsule which opens by a circular lid, the *operculum* (Fig 332, A, and B). Beneath the operculum in many species is a fringe of teeth which can be readily seen when the lid falls off (C). These teeth constitute the *peristome*. The peristome may consist of a double row of teeth, referred to as the inner and outer peristomes.

FUNARIA

The life history of a moss may be illustrated in the study of some form of simple structure, such as the common Cord Moss, *Funaria hygrometrica*. It may be found on earth, and in almost pure stands on cinders and heaps of ashes that have been left undisturbed for a season.

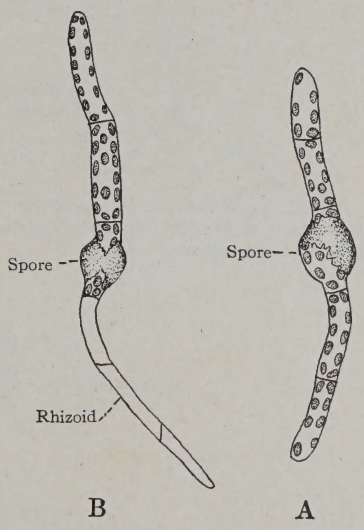


FIG. 333.—*Funaria hygrometrica*. Germinating spores. A, both germ tubes containing chloroplasts. B, one tube containing chloroplasts, while the other will function as a rhizoid.

The Germination of the Spore and the Development of the Gametophyte.—The wall of the spore consists of two layers, the outer brown *exospore* and the inner colorless *endospore*. During germination the exospore is ruptured, and the endospore protrudes as a papilla, or the cell may grow in two directions, sending out two germ tubes, one of which may become the first rhizoid (Fig. 333). With continued growth a system of numerous branches is produced resembling an alga. This system of alga-like filaments is the *primary protonema*. If rhizoids be exposed to the light, green branches, *secondary protonemata*, will be developed from them, and these will give rise to leafy axes. From the green protonemal filaments above the soil many special branches will arise, first as minute green buds, which develop into the well-known leafy axes, or moss plants (Fig. 334). In the tip of the green bud an apical cell is soon established, and from it the axis with its three rows of leaves will be developed.

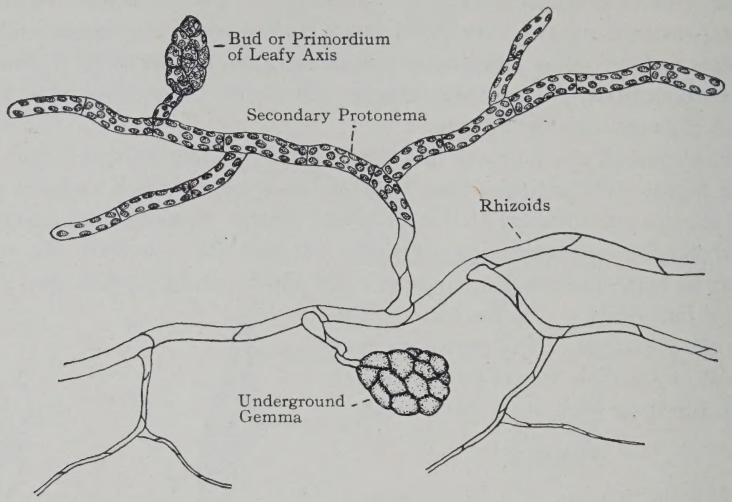


FIG. 334.—*Funaria hygrometrica.* Portion of a rhizoid from which has grown a secondary protonemal branch, bearing a bud or primordium of leafy axis, and an underground gemma.

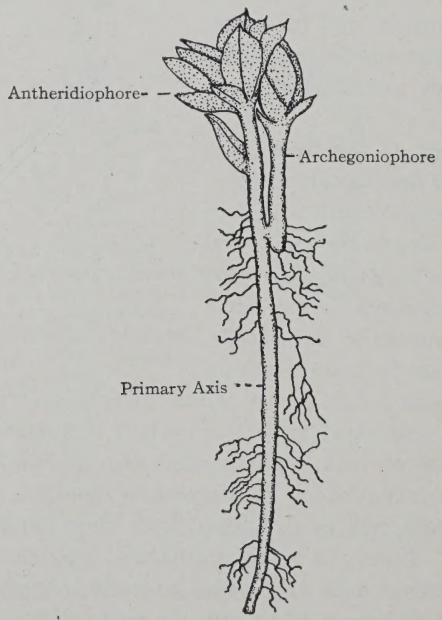


FIG. 335.—Gametophyte of Funaria. The primary axis which continues as the antheridiophore bears the archegoniophore as a branch. (After Boodle.)

The complete gametophyte consists of the leafy axes, rhizoids, and protonema. The protonema of the moss may be reasonably regarded as a juvenile form of the gametophyte capable of an unusually prolific vegetative propagation.

In Funaria the small green bud mentioned above will develop into a small primary leafy axis, the antheridiophore, which bears a number of antheridia at its tip. This young antheridiophore soon pro-

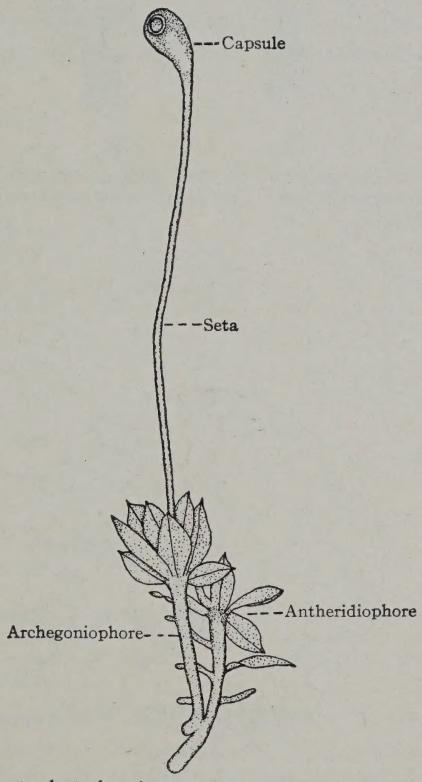


FIG. 336.—Gametophyte bearing immature sporophyte. (After Boodle.)

duces a branch, the archegonial branch, or archegoniophore, which bears the archegonia at its upper end and finally one sporophyte (Figs. 335, 336). The archegonial branch becomes much larger than the antheridial axis. As the antheridial axis ages the lower and older parts die and decay, thus severing the connection between the antheridiophore and the archegoniophore. Each branch may continue growth for a time as separate plants, being connected with the soil by the growth of numerous rhizoids (Fig. 337). This fact led to the view that Funaria was dioecious.

Each elongated leaf is pointed at the tip and possesses a midrib, the central cells of which serve as a conducting tissue (Fig. 338, A). The

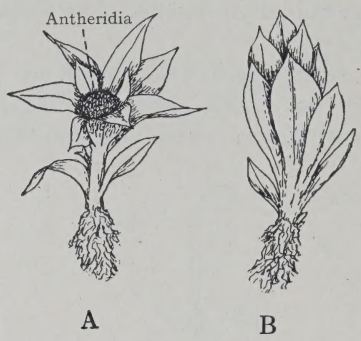


FIG. 337.—*Funaria hygrometrica*. A, antheridiophore with cluster of antheridia at tip of axis. B, archegoniophore. The archegonia, borne also at the tip of the axis are concealed by the leaves. × 7.

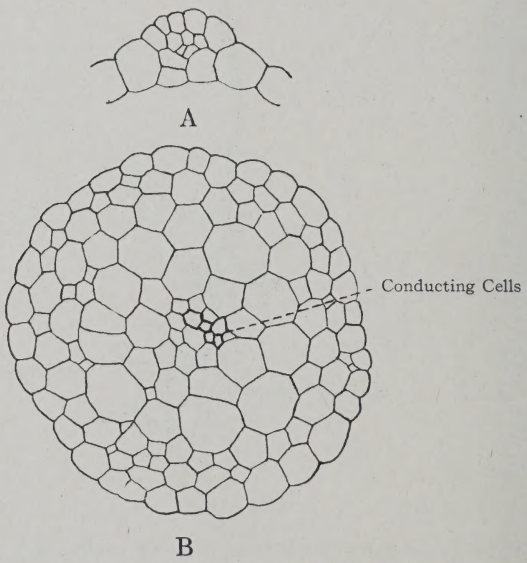


FIG. 338.—*Funaria hygrometrica*. A, cross section of midrib of leaf. B, cross section of axis of gametophyte.

rest of the leaf is made up of a single layer of cells containing numerous chloroplasts.*

As may be seen in a cross section, the axis is simple in structure (Fig. 338, B). In the center is a strand of smaller cells surrounded by

* The leaves of some mosses, such as Polytrichum, are more complex, in that several lamellae arise at right angles from the upper side and extend longitudinally. These greatly increase the photosynthetic tissue of the otherwise narrow leaves.

cells more or less uniform in character. The cells of the central strand are much elongated; they function as conducting tissue (Fig. 338). Beneath the epidermis the cells may be smaller and have thicker walls.

The growth of the axis proceeds, as a rule, from an apical cell which is in the form of a tetrahedron, or triangular pyramid, with its free surface somewhat rounded (Fig. 339, A). In a cross section, therefore, the apical cell will appear as a triangle (Fig. 339, B). From the three lateral faces of the apical cell are cut off by successive divisions three rows of cells, which give rise primarily to the axis and its leaves. In axes that branch, each branch springs from an initial cell that arises immediately below a leaf (Fig. 339, A).

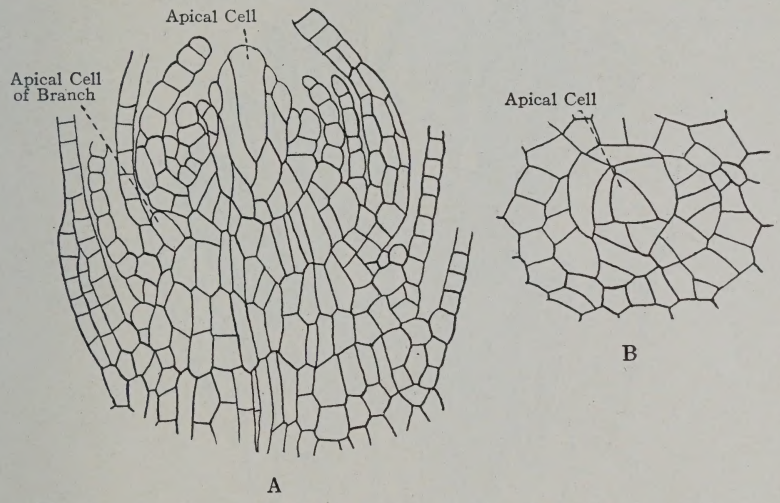


FIG. 339.—*Amblystegium riparium*, var. *fluitans*. A, median longitudinal section of the growing end of an axis. B, transverse section through the apex of the axis. (From Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

Vegetative Propagation of the Gametophyte.—As stated in a foregoing paragraph, if the rhizoids be exposed to the light, secondary protonemata will be developed from certain cells. On these filaments, as from primary protonemata, will arise small green buds, which develop into leafy shoots. Gemmae in the form of small brown buds are sometimes formed in the same way from rhizoids beneath the soil (Fig. 334). These are called resting buds. If exposed to the light, under growing conditions, they develop secondary protonemata, from which leafy shoots may spring. In some mosses gemmae are developed on the leaves. These may ultimately give rise to leafy plants. In some species the leafy axis may produce long, slender, creeping stolons with reduced leaves, and these axes may give rise to upright leafy branches.

Sex Organs.—The antheridiophore is smaller than the archegoniophore and may be recognized by the more loosely arranged leaves and by the presence of a group of reddish antheridia at the apex of the axis surrounded by a rosette of leaves (Fig. 337, A). The antheridia are more clearly seen in a longitudinal section of the tip of the axis (Figs. 340, 341).

Each antheridium is club-shaped, possessing a short stalk. The wall consists of a layer of relatively large cells that may contain reddish bodies. Within is a large number of very small cells which give rise to the sperms. The latter are similar to those of the liverworts (Fig. 342, D). When the

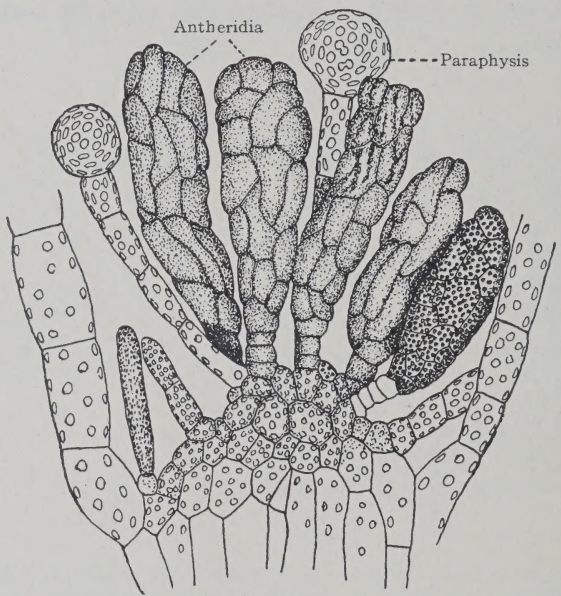


FIG. 340.—*Funaria hygrometrica*. Longitudinal section through tip of an antheridiophore, showing antheridia in surface view, and paraphyses. (From Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

mature antheridium becomes wet the sperms are expelled in a mucilaginous substance derived largely from the walls of the sperm-bearing cells.

The archegoniophore is larger than the antheridiophore and has larger and more closely set leaves (Fig. 337, B). The archegonia are flask-shaped like those of the liverworts, though much larger. They are borne at the apex of the stem (Fig. 342, A, B). In some mosses the antheridia and archegonia may be borne together in the same cluster.

Fecundation and Development of the Sporophyte.—The processes involved in the opening of the archegonium and in the union of egg and sperm are the same as in the liverworts.

Unlike that of the liverwort, however, the sporophyte develops into a long, slender cylindrical rod while still covered by the enlarged venter of the archegonium (Fig. 343). At this stage of development it may be recognized as a small green rod emerging from the end of the leafy axis (Fig. 344, A, *s*).

The young sporophyte grows rapidly in length, and severs the archegonium from the stem (Fig. 344, B-D). The wall of the archegonium, now known as the *calyptra* (*c*), is carried upon the distal end of the sporophyte. The sporophyte, at this stage, appears to the unaided eye as a slender

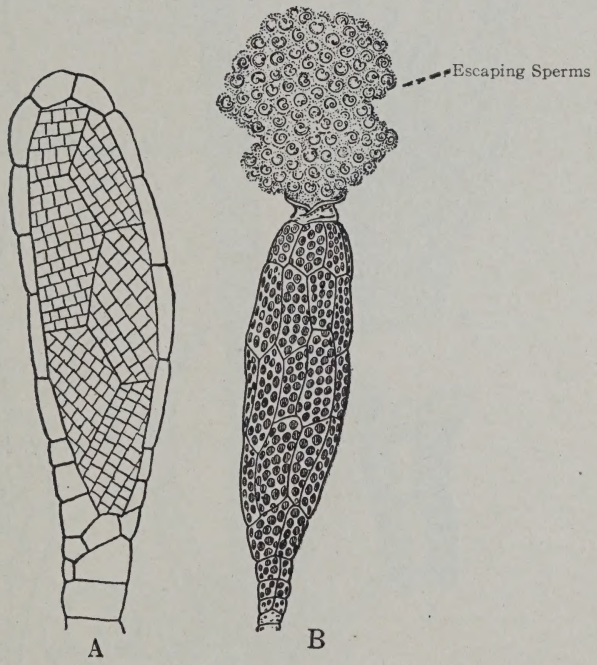


FIG. 341.—*Funaria hygrometrica*. A, longitudinal section of an immature antheridium. B, surface view of antheridium from which sperms are escaping. (B, after Sachs.)

thread arising from the end of the gametophore. With further growth the distal end of the sporophyte, which is covered by the calyptra, enlarges greatly and becomes differentiated into the capsule (D, *b*). In Funaria the calyptra may fall off before the capsule is mature.

Beneath the calyptra is seen the lid, or operculum. When the operculum falls off, the peristome is seen as a fringe of triangular, brown teeth, as mentioned in a preceding paragraph. The peristome of Funaria is double, the inner being inconspicuous. The teeth of the outer peristome represent strips of cell wall conspicuously marked by horizontal thicken-

ings (Fig. 345, B, *o*). In the Hairy-Cap Moss, *Polytrichum commune*, each tooth of the single peristome consists of a cell. The thin gray membrane stretched across the mouth of the capsule is the *epiphragm* (Fig. 346, B, *e*).

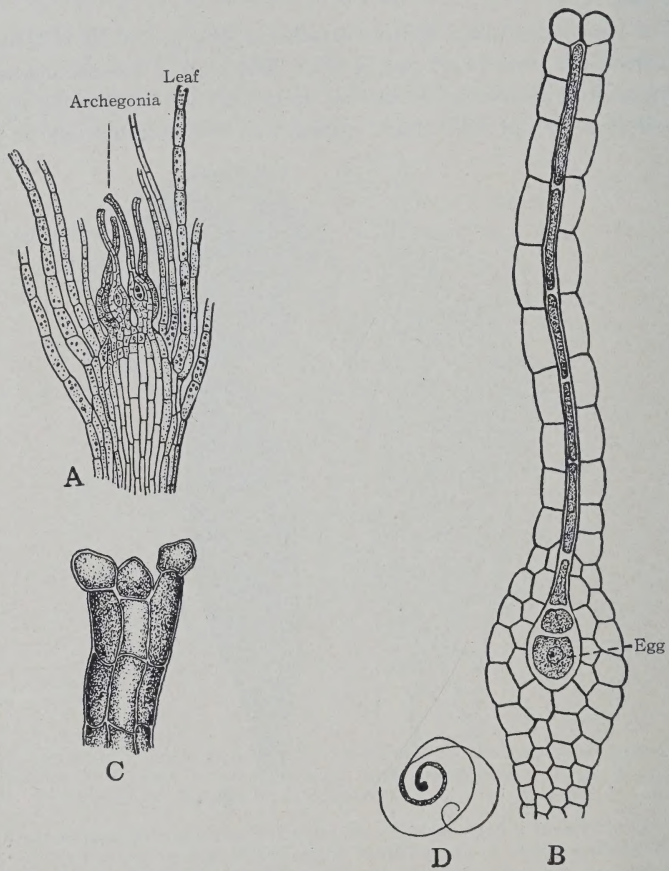


FIG. 342.—*Funaria hygrometrica*. A, longitudinal section of tip of archegoniophore, showing cluster of archegonia. B, longitudinal section of archegonium. C, tip of neck of open archegonium. D, sperm. (A, C, D, from Goebel.)

Structure of the Capsule.—The structure of the capsule before it reaches maturity may be understood from a median longitudinal section (Fig. 345, A). It is seen that the capsule consists of an outer wall three layers of cells in thickness and a central mass of tissue, with a large air space between them. The central mass is continuous with the upper part of the capsule, and is connected with the wall and bottom of the capsule by slender filaments of chlorophyll-bearing cells. On either side

of the inner mass, near its surface, is a row of spore-bearing tissue. The large, thin-walled cells comprising the inner part of the mass constitute the columella. The spore-bearing layer is consequently in the form of a cylinder, with the columella extending through it above and below.

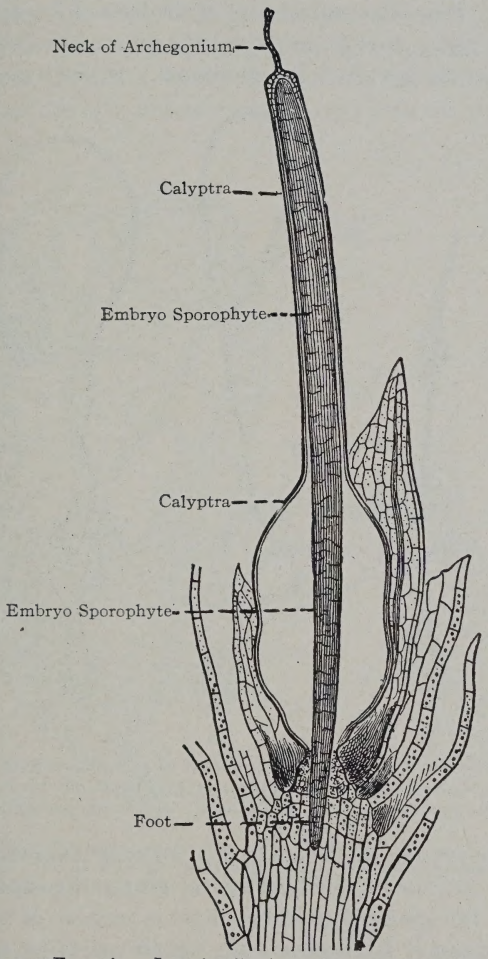


FIG. 343.—Funaria. Longitudinal section of an embryo sporophyte enclosed in the venter of the archegonium (calyptra) before the latter has been broken away from the axis of the gametophore. The lower end (foot) of the sporophyte has grown down into the tip of the axis of the gametophore. (From Sachs, "Lectures on the Physiology of Plants," Clarendon Press.)

Between the spore-bearing cells and the air space is a layer of tissue three cells in thickness.

The upper end of the capsule is covered by the operculum. The large, conspicuous cells at the base of the operculum constitute the annulus.

By the mechanical action of the annulus the operculum is separated from the rest of the capsule. Beneath the operculum is the peristome.

The lower part of the capsule, which narrows into the seta, is the *apophysis*. Its loosely arranged cells contain chlorophyll and represent photosynthetic tissue. From the central part of the base of the apophysis a strand of conducting tissue extends down into the seta. The outer layer of small cells with rather thick walls is the epidermis. In the region of the

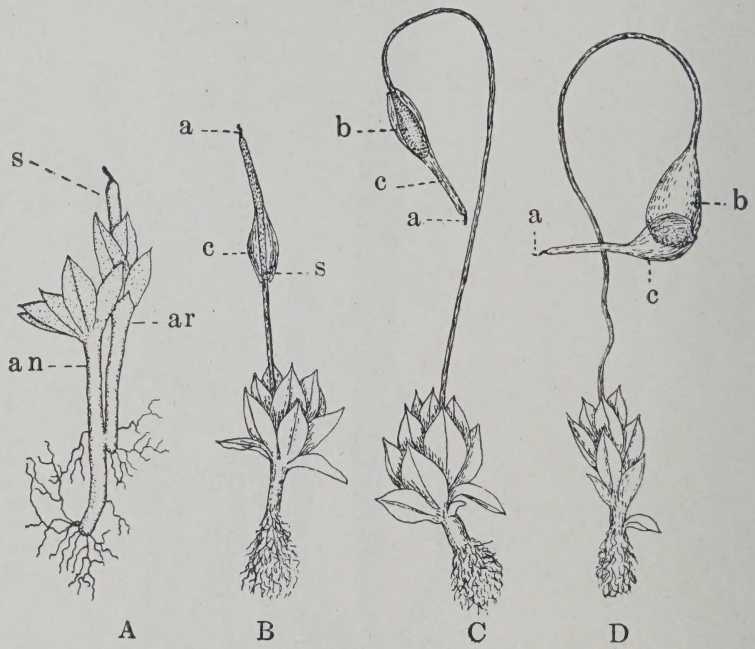


FIG. 344.—*Funaria hygrometrica*. A–D, development of the sporophyte, the capsule forming in the last two figures; *an*, antheridophore; *ar*, archegoniophore; *a*, shrivelled neck of archegonium; *s*, young sporophyte; *c*, calyptra; *b*, capsule of sporophyte.

apophysis, stomata are present in the epidermis, forming communications between the outer air and the intercellular spaces within the capsule.

As in Anthoceros, the sporophyte of the moss is capable of making a part of its own food, and it is therefore not wholly parasitic upon the gametophyte. The lower end of the seta, the *foot*, is thrust a short distance down into the end of the axis of the gametophyte.

Formation of the Spores.—The spore-bearing tissue finally gives rise to large, rounded cells, which, because of the enlargement of the capsule, separate from one another. These are the spore mother-cells, from each of which, by division, is formed a tetrad of spores. The first of the two nuclear divisions in the spore mother-cell is the reducing division.

Each spore, and every cell of the resulting gametophyte, contains the single number of chromosomes.

Ripening of the Capsule.—When the sporophyte reaches maturity the water supply is cut off from below, and all the cells, except the spores, die and dry up. The cells of the columella and inner part of the operculum, as well as those within the epidermis, collapse completely, leaving little more than the spores themselves, the firm cell walls of the peristome, and the cells connecting the latter with the wall of the capsule. By

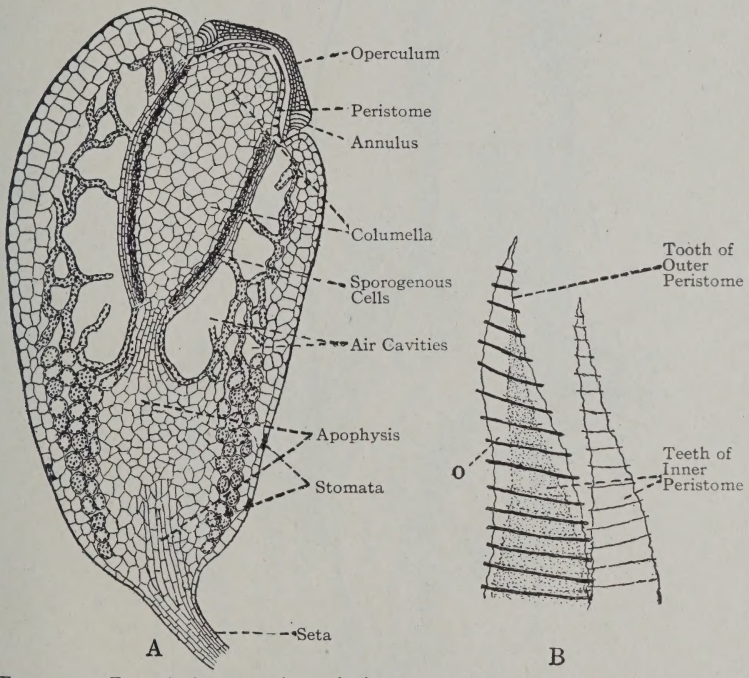


FIG. 345.—*Funaria hygrometrica.* A, longitudinal section of immature capsule of sporophyte. B, part of the peristome; *o*, outer peristome behind which a tooth of inner peristome is shown stippled.

the breaking down of the thin lateral and transverse walls of the cells that give rise to the peristome, the outer and inner thickened walls of these cells are separated, and form the two rows of membranous teeth that surround the mouth of the capsule. The small cells between the annulus and the margin of the capsule become dry, and by the mechanical action of the annulus the operculum is disconnected and falls off. The ripe capsule consists finally of a thin, dry, urn-like shell with a large cavity containing the spores.

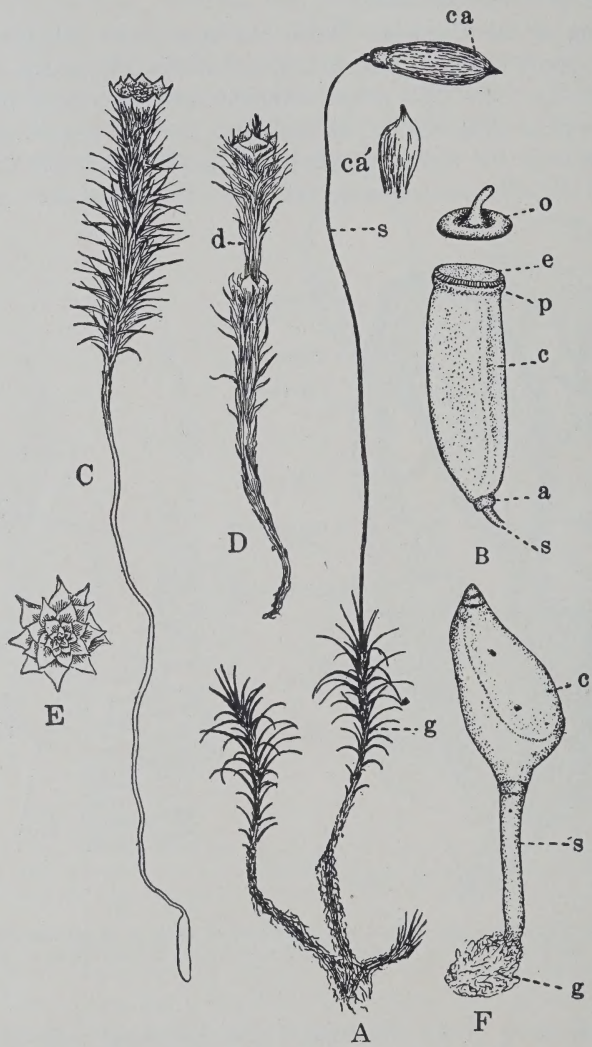


FIG. 346.—The hairy-cap moss, *Polytrichum commune*, A–E. *Buxbaumia aphylla*, F. A, female plant bearing a sporophyte. B, capsule enlarged; *a*, apophysis; *c*, capsule; *ca*, calyptra; *ca*^{1}, calyptra removed; *e*, epiphragm; *p*, peristome; here each tooth of the peristome is a whole cell. C, male plant. D, male plant which has continued growth after bearing a crop of antheridia. E, end of male plant viewed from above. F, Buxbaumia, one of the rare and peculiar mosses; the gametophyte (*g*) does not develop real leaves; *c*, capsule; *s*, seta. (C, D, E, from Gager's "General Botany." By permission of P. Blakiston's Son and Company, Publishers.)

Among the large moss plants to be found in the woods are the hairy-cap moss, Polytrichum (Fig. 346), and the pigeon wheat moss, Catharinea (Fig. 347).

FIG. 347.—A common rather large moss, *Catharinea undulata*. Note the large branched gametophores bearing sporophytes. (From Sachs, "Lectures on the Physiology of Plants," Clarendon Press.)

In the remarkable moss, Buxbaumia, the gametophyte is a very small flat structure, scarcely visible to the unaided eye, while the sporophyte is large and well developed. At a glance it resembles a bug on a stick (Fig. 346, F).

Classification of Musci

The Musci are grouped in three orders, Sphagnales, Andreaeales, and Bryales. In the following only a few of the genera that contain the more familiar and common mosses are given.

Order 1. Sphagnales
- Sphagnum, Peat Moss, or Bog Moss.

Order 2. Andreaeales
- Andreaea

Order 3. Bryales, True Mosses
- Funaria, Cord Moss
- Catharinea, Pigeon Wheat Moss
- Mnium
- Polytrichum, Hairy Cap Moss
- Climacium, Pine Tree Moss
- Rhodobryum
- Hypnum, Plume or Feathery Moss
- Buxbaumia
- etc.

SPHAGNALES

All of the Sphagnales are included in the genus Sphagnum. They are commonly found in swampy localities known as bogs, where the partly decayed moss may contribute to the formation of peat. The pale green leaves are borne mainly on the numerous short branches (Fig. 348, A). The leaves do not have a midrib. Each when mature consists of two kinds of cells, large colorless cells, between which are long, narrow living cells containing chloroplasts. The large colorless cells are devoid of living contents; their walls usually possess spiral or ring-shaped thickenings on the inside. Round holes are generally present in their walls (Fig. 348, B). Similar colorless cells form the cortex of the stem. There is no central differentiated strand of cells in the stem as in the true mosses. The colorless cells of both leaf and stem have a remarkable capacity to take up water, so that the whole plant retains water like a sponge.

The sporophyte has no seta. The slender, naked stalk bearing the sporophyte is the leafless elongation of the axis of the gametophyte, known as the *pseudopodium*. The pseudopodium is *analogous* to the seta of the Bryales but not *homologous* with it. The sporophyte resembles that of Anthoceros in the possession of a columella overarched by the spore-bearing tissue, and a bulbous foot. The capsule has an operculum, resembling in that respect the capsule of the Bryales.

The gametophyte of Sphagnum is monoecious in some species and dioecious in others. In the monoecious species the antheridia and archegonia are borne on different branches.

Sphagnum is used as packing material and for many other purposes. During the world war certain species were used along with other materials in making surgical dressings.

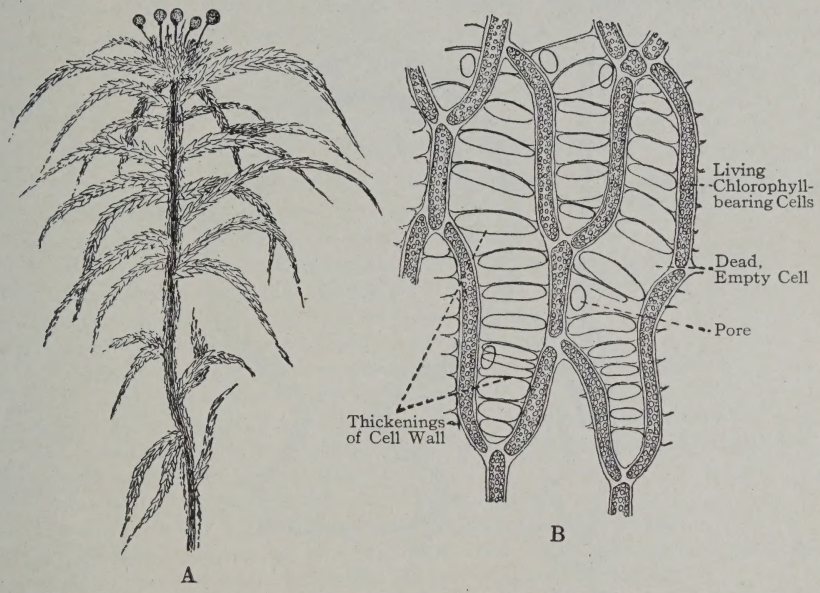


FIG. 348.—Sphagnum. A, habit of fruiting plant. B, a few cells of leaf, consisting of long, narrow living cells with chloroplasts and large colorless dead cells, whose walls have spiral, or ring-like, inner thickenings and round pores or openings.

The protonema is thalloid, resembling a small liverwort of simple structure.

ANDREAEALES

This order includes a group of small mosses intermediate in character between the Sphagnales and the Bryales. The capsule opens by longitudinal slits. The sporebearing tissue extends over the columella somewhat as in Sphagnum.

BRYALES

This order contains the vast majority of mosses. The numerous species are grouped under several families and in many genera. A few genera, to which some of the more commonly known mosses belong, are listed in a preceding paragraph.

Summary.—The chief points in the life history of the liverwort and moss may be compared in the summary shown at foot of page.

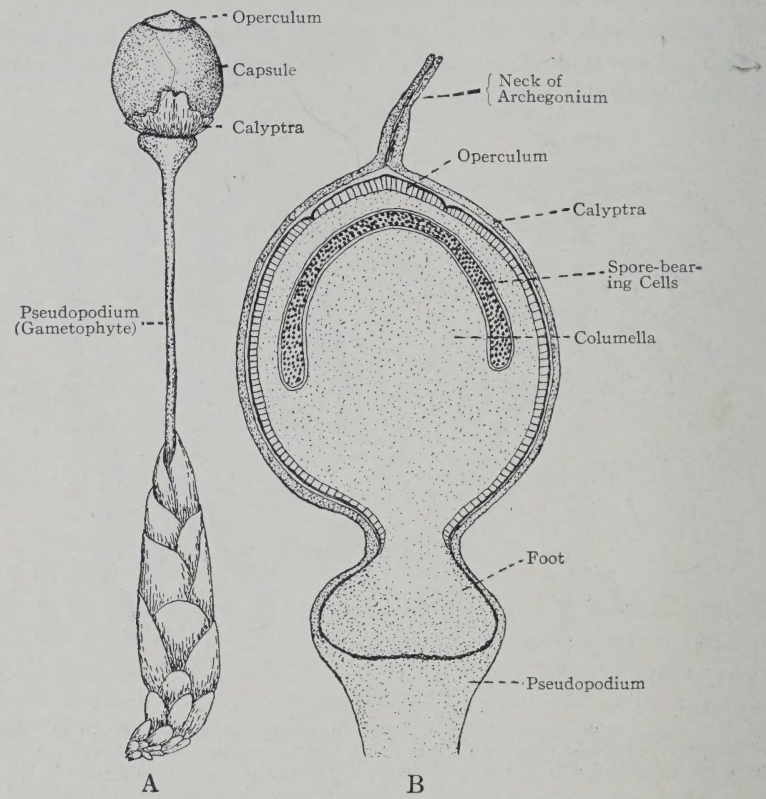


FIG. 349.—Sphagnum. A, short branch bearing sporophyte on the elongated gametophytic stalk, the pseudopodium. B, median section through sporophyte and upper end of pseudopodium. (A, from Schimper; B, from Waldner.)

Gametophyte

LIVERWORT	MOSS
1. Flat thallus or leafy axis, dorsiventral.	1. Leafy axes, generally upright, arising from protonemata.
2. Leaves without a midrib.	2. Leaves with a midrib.
3. Rhizoids unicellular, unbranched.	3. Rhizoids multicellular, branched.
4. Much larger than sporophyte.	4. About as large as sporophyte.

Sporophyte

1. A capsule or a stalk and simple capsule.	1. Long stalk (seta) and a highly differentiated capsule.
2. Elaters present except in Riccias.	2. No elaters present.
3. Capsule splits open by valves.	3. Capsule opens by a lid, the operculum.

The most outstanding feature in the evolution of the plant kingdom, in passing from algae and fungi to the Bryophyta, is found in the distinct and definite character of the well differentiated haploid and diploid structures, to which the terms gametophyte and sporophyte have been applied. These terms are scarcely applicable to the algae and fungi, because in many algae and fungi the limits of haploid and diploid structures are not definitely known. The zygote is always diploid, but the complete diploid structure cannot always be determined with accuracy in the algae. Moreover, the step in the life cycle at which diploid changes to haploid is not known with certainty in but comparatively few algae.

TOPICS FOR REVIEW AND DISCUSSION

What is the haploid structure of the liverwort called? The diploid structure? Why are those terms appropriate?

What is the derivation of the word Hepaticae?

What is meant by alternation of generations? Do you know of any alga to which those terms could be appropriately applied? Do you think the terms sporophyte and gametophyte should be applied to the algae and fungi?

What is a monoecious gametophyte? A dioecious gametophyte?

What physiological relation does sporophyte sustain to gametophyte?

Are the antheridia and archegonia gametangia?

What is the calyptra and from what organ of the gametophyte is it derived?

What would enable you to distinguish a moss gametophyte from a liverwort gametophyte which consists of a leafy axis?

What constitutes vegetative propagation in the liverwort and moss?

What are gemmae? Gemma cups? Are gemmae present in mosses?

Both sides of the gemma of Marchantia are alike. When it grows into an older gametophyte what determines which side will be the upper or dorsal side?

What step in the life cycle of a moss or liverwort requires that the plant be wet? Why?

In Marchantia how do the sperms get across from antheridial disk to archegonial disk?

In what liverwort are the sperms forcibly discharged?

Does the moss sporophyte reach maturity within the calyptra?

What becomes of the calyptra?

Is the operculum a part of the gametophyte or sporophyte?

In what liverworts are there no elaters?

What do the elaters accomplish in Marchantia and Porella, which is useful to the plant?

Do mosses possess elaters?

What family of liverworts has the most complex gametophyte? What family has the simplest gametophyte? Which has the simplest and which the most highly differentiated sporophyte?

What is a spore mother-cell? A spore tetrad?

Where does the numerical reduction in the number of chromosomes to one-half take place?

Using the live cycle diagram of Porella as a suggestion, write a life cycle diagram of a moss.

Have you any reasons for thinking that liverworts were evolved from algae?

What do you think would have to happen in order that any alga you know might be changed to the status of a liverwort?

What evidences of evolution do the sporophytes of the liverwort and of the moss reveal to you?

What are analogous structures?

What are homologous structures?

Are the archegonia of liverworts and mosses homologous?

Is what appears to be seta in Sphagnum homologous to the seta of Funaria or Polytrichum?

What peculiar moss is said to suggest a bug on a stick? What kind of a gametophyte has it?

What is peat? Peat moss? How is peat made? Can you mention several economic uses of peat? Of Sphagnum moss?

What role do mosses play in the economy of nature?

What is the function of the peristome?

What are primary protonemata? Secondary protonemata?

Why are mosses so much more abundant than liverworts.

What evolutionary advance has the moss sporophyte made above the liverwort sporophyte?

In passing from Liverwort to moss, which structure, haploid or diploid, tends to increase relatively in size?

What is meant by the expression, progressive sterilization of tissue, in the evolution of the sporophyte in the Bryophyta?

CHAPTER XVII

PTERIDOPHYTA

The plants commonly known as ferns (Filicinae), horsetails or scouring rushes, (Equisetinae), and club mosses (Lycopodinae) belong to the Pteridophyta. They are distinguished from the liverworts and mosses by the fact that the sporophyte becomes an independent, long-lived plant differentiated into true *root*, *stem*, and *leaf*, each of these organs possessing a well developed *vascular system*. In the ferns the gametophyte, *prothallium*, is usually a small, heart-shaped structure which produces but one sporophyte, although several sporophytes may be made to develop from one gametophyte under experimental conditions in the laboratory. The gametophyte nourishes the sporophyte until the latter has become self-supporting in the production of one or more leaves and one or more roots. Soon after this condition has been attained by the sporophyte, the gametophyte becomes exhausted and dies. The gametophyte and the sporophyte are the haploid and diploid structures respectively.

CLASS I. FILICINAE

The Life History of the Fern

Any of the ordinary ferns belonging to the family, Polypodiaceae, will serve to illustrate the life history.

The Sporophyte.—The plant which we usually regard as the fern is the sporophyte. Its stem, which is a rhizome, grows horizontally, as a rule, near the surface of the ground. It is dark brown in color, being covered by a coat of small brown scales which develop also upon the leaf stalks. Stem branches arise back of the growing point, and new leaves develop annually from the growing end or ends. The oldest parts of the stem gradually die and decay.

When the stem is horizontal, the leaves spring mainly from the upper surface and the roots from the lower (Fig. 350, A). If the stem be upright as in the evergreen fern, *Dryopteris marginalis* (*Aspidium marginale*), the leaves form a crown encircling the end of the stem. The young leaf is coiled up in the bud, like a watch spring. The veins may be free or form a network of anastomosing branches.

Ordinarily the roots are much branched and arise near the bases of the leaves or from the bases of the leaves. In tree ferns the roots may form a thick matted mass covering the stem.

FIG. 350.—Habit sketch of the fern, *Aspidium filix-mas*. A, stem with young (rolled up) and mature leaves. The dots on the leaflets are sori. B, a leaflet with sori, each covered by a shield-like indusium. C, a section through a leaf blade and sorus. D, sporangium. (Adapted from Wassidlo.)

The Sporangium.—The sporangia are borne either on foliage leaves or on leaves completely modified into purely spore-bearing structures.

The sporangia are aggregated in clusters, *sori*, and each sorus is usually covered by an outgrowth of the leaf, an *indusium* (Fig. 351, A, B). A sorus always arises in connection with a vein (Fig. 350, C). In the Maiden-

hair fern (Adiantum) the sporangia are covered by the folded-over margin of the leaflet, which constitutes a *false indusium* (Fig. 351, C). Each sporangium consists of a flattened body, or capsule, borne on a slender stalk (Figs. 350, 352). The wall of the sporangium consists of a single layer of cells. Around the edge is a row of modified cells, the ring, or *annulus*, which, by a mechanical action, opens the sporangium. The place of dehiscence, or opening, is indicated at one side by two narrow cells that form the *stomium*.

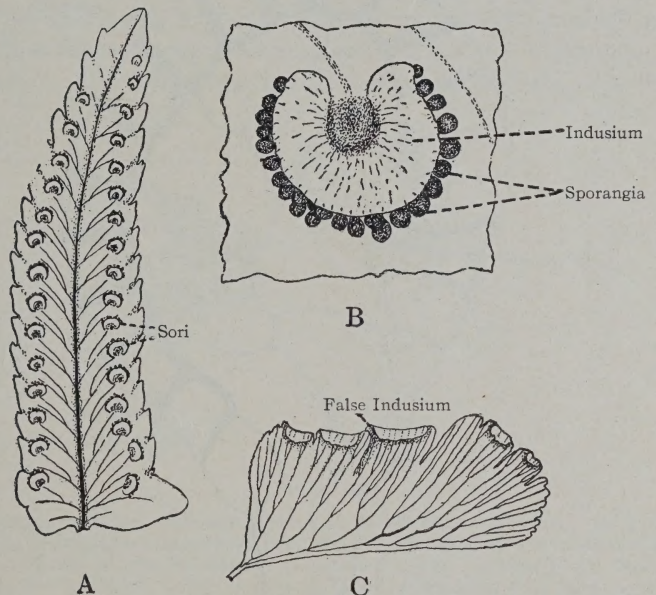


FIG. 351.—Spore-bearing leaflets of common ferns. A, B, Boston fern (*Nephrolepis exaltata*). C, Maidenhair Fern (*Adiantum pedatum*). A, pinna with sori. B, enlarged sorus with indusium. C, pinna with sori covered by the folded margin of the leaflet, a *false indusium*.

Opening of the Sporangium.—Dry weather is necessary for the opening of the sporangium. As will be seen in Fig. 352, the cells of the annulus have thick radial and inner walls, while the outer walls are thin. The thickened inner and radial walls form U-shaped curves. When the mature sporangium dries, the annulus straightens out slowly and breaks the capsule open transversely at the stomium. The straightening process continues to such a degree that the annulus bends back upon itself, or turns inside out (Fig. 353, A), when, with a sudden snap or jerk, it returns to its original position (Fig. 353, B). This catapult-like action tosses the spores out into the air. The process may be repeated, and in this manner the spores may be expelled.

The annulus is everted when the parallel sides of the U-shaped cells come close together, bending the thin outer walls, as shown in Fig. 353, C. The shape of the cells of the annulus before the sporangium opened is shown at D.

The Germination of the Spore and the Development of the Gametophyte, or Prothallium.—For a study of the gametophyte we shall select

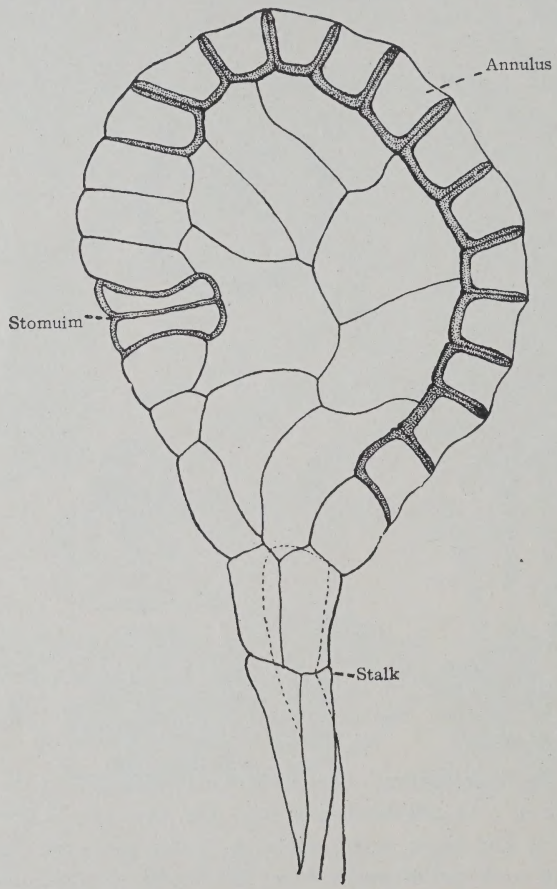


FIG. 352.—Mature sporangium of *Nephrolepis exaltata*, in surface view.

the Ostrich Fern, *Onoclea struthiopteris*, (*Matteuccia nodulosa*). The spore has a wall consisting of three layers, namely, the outer, brown *perinium*, the middle layer, *exine*, or *exospore*, and the inner cellulose layer, *endospore*, or *intine*. The exospore and endospore are colorless.

As the spore germinates, the perinium bursts and often falls away. The exospore is also ruptured, but the endospore remains as the wall of

the growing cell (Fig. 354, A, B). A papilla is now sent out through the rupture in the exospore. The cell divides, cutting off the papilla as a small cell, which grows into the first rhizoid (Fig. 354, C). The larger cell now begins development into the body of the gametophyte. By rapid growth and division, a short row of cells is soon formed (D). If the spores are grown on water, a more filamentous and irregular structure will result.

At a very early stage in development, an oblique division will occur in one of the distal cells, thus establishing a V-shaped apical cell (Fig. 354, E). This apical cell, by further successive divisions, cuts off cells alternately from the two sides. Such an apical cell is said to possess two "cutting faces." The subsequent growth and division of the cells thus

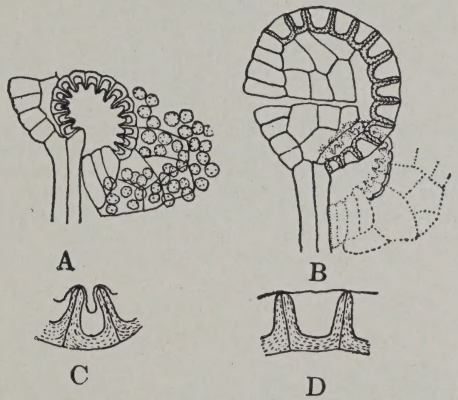


FIG. 353.—A, sporangium with annulus turned inside out, or everted. B, similar sporangium after recovery by a sudden snap or jerk. C, condition of cells of the annulus when everted. D, cell of annulus before sporangium opens. (From F. O. Bower's "Botany of the Living Plant." By permission of the Macmillan & Company, Ltd., Publishers.)

formed from the apical cell give rise to two symmetrical wings, or lobes, of the prothallium, and the result is the conventional heart-shaped plant (Fig. 355, A, and 356).

At a later stage in development than that shown in Fig. 355, A, the V-shaped apical cell divides transversely into two cells, a larger, outer, rectangular cell, and an inner cell triangular in surface view (Fig. 355, B). The outer cell now has three cutting faces. It can divide by cutting off cells from both the right and left sides, and from the inner side or end. The outer, or anterior side of this cell is rounded in a dorsiventral direction (Fig. 359). By longitudinal divisions this cell may give rise to several apical cells, the number depending on the width of the apical sinus (Fig. 356). The cells cut off from the inner ends of the apical cells divide in three planes, thus giving rise to the more massive midrib,

or archegonial cushion. The wings of the prothallium remain one cell in thickness.

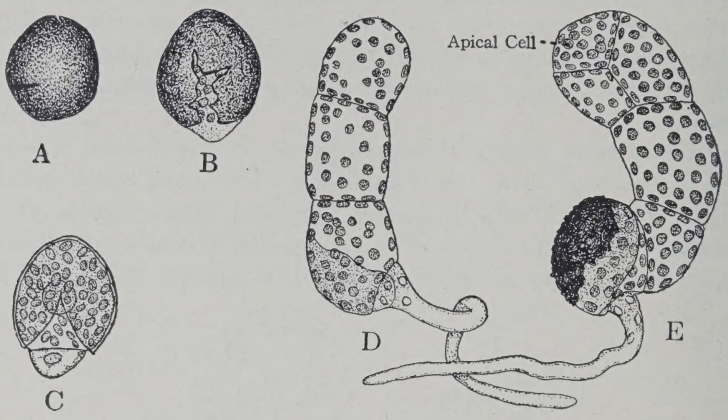


FIG. 354.—*Matteuccia nodulosa.* Germinating spores and early stages in the development of the prothallium. A, spore before rupture of wall. B, bursting of perinium. C, the perinium has fallen away, the exospore is ruptured, and the papilla to form the first rhizoid is cut off. D, the spore has given rise to a 3-celled prothallium with one rhizoid. E, prothallium in which the apical cell has been established.

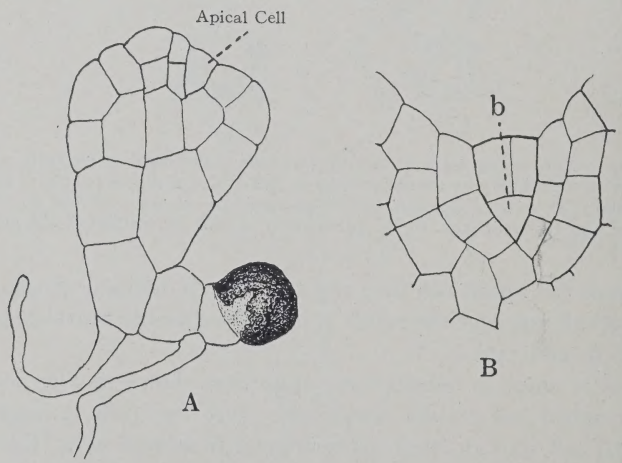


FIG. 355.—*Matteuccia nodulosa.* A, young prothallium which is becoming heart-shaped. B, apical region in which the V-shaped apical cell has given rise to rectangular apical cells with three cutting faces; *b*, the cell cut off from the pointed end of the V-shaped cell.

From the margin and under surface of the posterior part of the prothallium, numerous one-celled rhizoids develop. As soon as the midrib is established, the prothallium is large enough to bear archegonia.

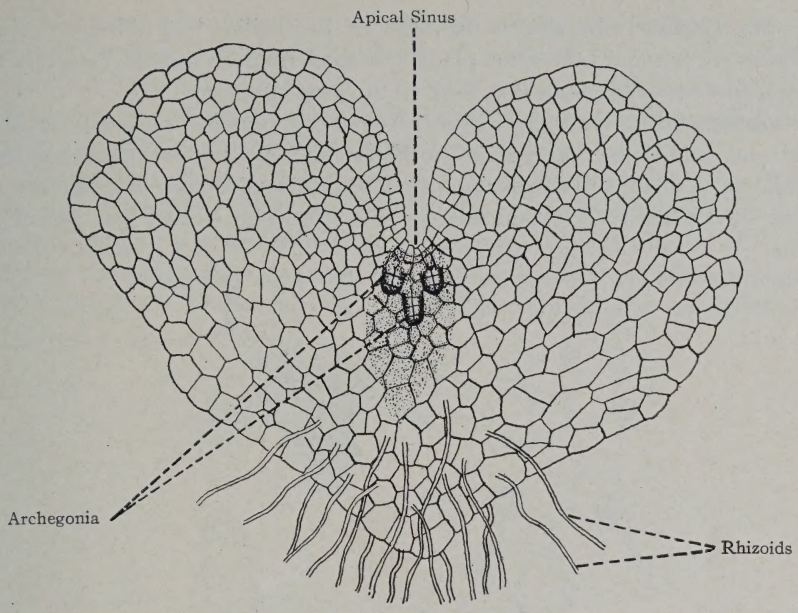


FIG. 356.—*Matteuccia nodulosa*. A female prothallium bearing three archegonia near the growing edge, or apical sinus.

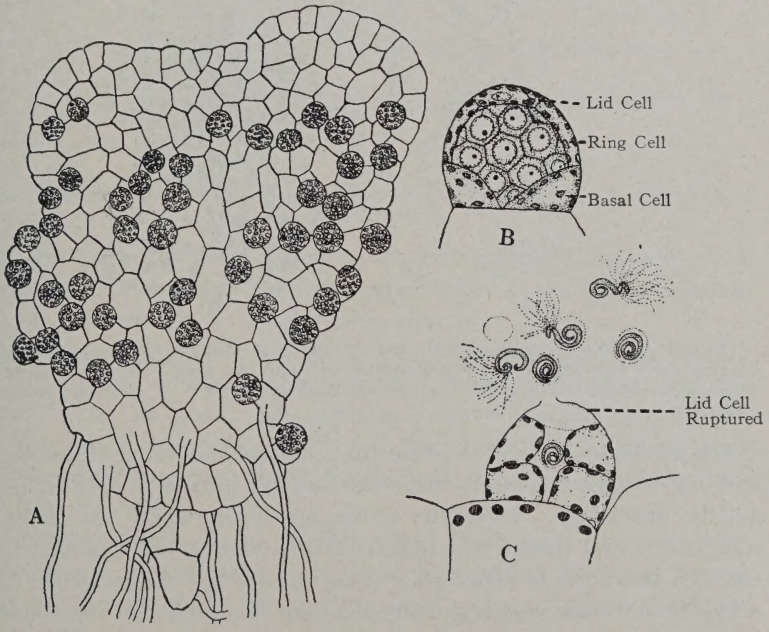


FIG. 357.—A, male prothallium of *Matteuccia nodulosa*, bearing many antheridia. B, immature antheridium; C, antheridium from which sperms have escaped.

Sex Organs.—In strictly monoecious prothallia, both kinds of sex organs are borne on the same plant, the antheridia on the older posterior part, and the archegonia just back of the growing point.

Antheridium.—In many ferns it frequently happens, especially under cultural conditions, that certain prothallia will begin to develop antheridia while quite small, and these organs may be produced in such large numbers that the plants never attain a larger size (Fig. 357, A, and Fig. 358, A).

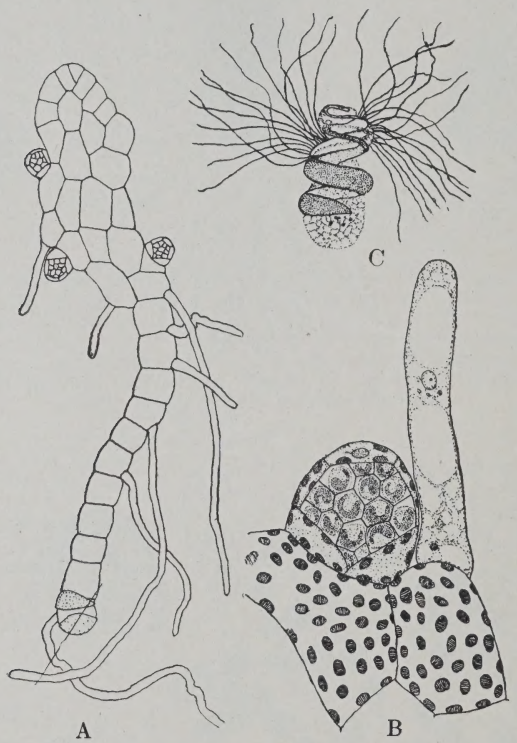


FIG. 358.—*Matteuccia nodulosa*. Antheridia and sperms. A, small prothallium bearing three antheridia. B, two marginal cells and one young rhizoid of prothallium with one antheridium, in which sperms are about half grown. C, a sperm, very highly magnified.

Other prothallia will, on the contrary, produce few or no antheridia, but continue to grow to a larger size, when both sex organs, or only archegonia, will be developed. When the spores are sown thickly on earth, large numbers of the plants will remain small, bearing only antheridia. In *Onoclea struthiopteris* (*Matteuccia nodulosa*) and *Onoclea sensibilis*, there is a tendency toward dioecism under the most favorable cultural conditions, but all prothallia are potentially bisexual.

The antheridia are borne at the margins and on both surfaces. They are usually hemispherical or thimble-shaped. The wall of the antheridium consists of three cells, a basal (funnel-shaped) cell, a middle (ring-shaped) cell, and a lid cell (Fig. 357). These three enclose a mass of cells, the sperm initial cells, which will give rise to the sperms.

The mature sperm is a spiral-shaped body bearing many cilia (Fig. 358, C). The larger, posterior part of the sperm is derived from the nucleus, while the anterior portion comes from the cytoplasm. At the edge of the cytoplasmic portion is a delicate thread, the *blepharoplast*, which bears the numerous cilia. Partly surrounded by the posterior

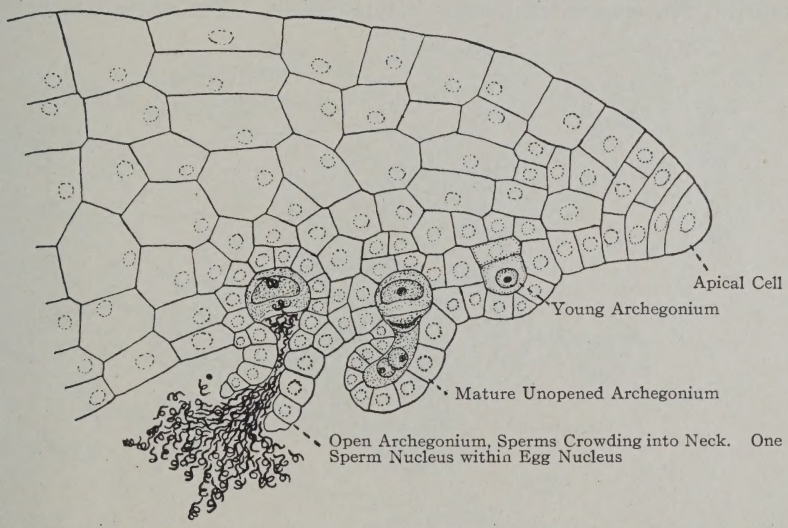

Apical Cell
Young Archegonium
Mature Unopened Archegonium
Open Archegonium, Sperms Crowding into Neck. One Sperm Nucleus within Egg Nucleus

FIG. 359.—*Matteuccia nodulosa*. Longitudinal vertical section through the growing point of the prothallium.

turns of the sperm is a large vesicle which may contain starch and other food granules. The sperm is, therefore, merely a naked cell so transformed as to be capable of locomotion in water.

When the antheridium is mature, the application of water will lead to its opening by the bursting, or separation, of its lid cell (Fig. 357, C). The sperms are expelled by the pressure exerted against them by the turgid basal and ring cells. Free from the antheridium, each sperm escapes almost immediately from the delicate, colorless membrane surrounding it and swims away.

The Archegonium.—In our ordinary ferns (Polypodiaceae) the archegonia are borne on the under side of the prothallium just back of the growing point, although a few may be developed on the dorsal side as well (Fig. 359).

The mature archegonium is flask shaped, but smaller and more simple in structure than that of the moss. Its venter is embedded in the tissue of the midrib, only the neck protruding beyond the surface. The fully formed archegonium consists of an axial row of cells surrounded by a single layer of cells. The lowest, or innermost, of the axial row of cells, which lies in the venter, is the egg. Above it is the small ventral canal cell, and extending up into the neck is the neck canal cell (Fig. 359). The neck is generally curved backward or to one side. The wall of the neck consists of four rows of cells. The egg and ventral canal cell are sisters. In the neck canal cell are almost invariably found two nuclei in Onoclea, Matteuccia, and other Polypodiaceae. The ventral canal cell

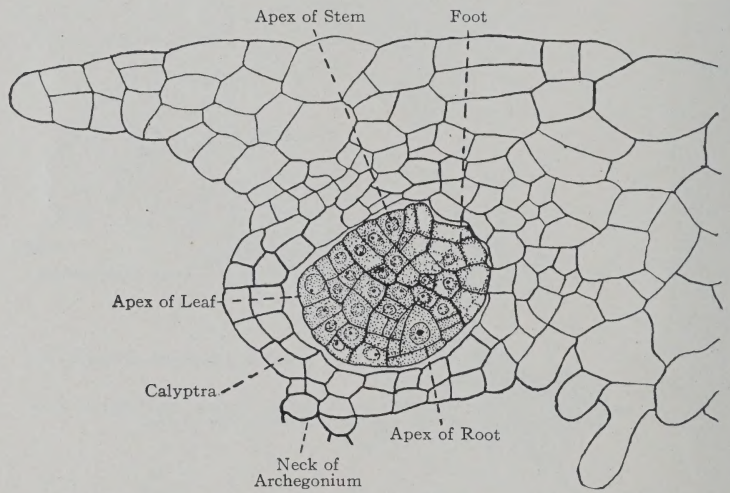


FIG. 360.—*Matteuccia nodulosa.* Longitudinal vertical section of a gametophyte containing embryo sporophyte in which the four regions, leaf, stem, root, and foot are clearly differentiated.

and neck canal cell undergo mucilaginous degeneration as the archegonium matures.

Fecundation.—Application of water to the ripe archegonium causes it to open. The end cells of the neck separate, and the mucilaginous contents begin to diffuse out into the water. This substance exerts a positive chemotactic stimulus on the sperms, so that if any approach the open neck, they will enter and pass down to the egg. The entire sperm enters the cytoplasm of the egg, where its cytoplasmic portion remains, while the nucleus of the sperm passes into the nucleus of the egg (Fig. 359). Within the nucleus of the egg that of the sperm gradually breaks up into smaller particles, so that finally the particles of the two nuclei can no longer be distinguished from one another. Fecundation is then complete.

Development of the Embryo Sporophyte.—Soon after fecundation the venter of the archegonium closes, whereas the neck dies and turns brown. A cellulose wall is formed about the zygote, which begins growth and division immediately. The first division of the zygote is parallel with the long axis of the archegonium. The two resulting hemispherical cells divide simultaneously in a plane at right angles to the first division wall. The embryo now consists of four cells, or quadrants, each of which is the starting point of one of the four definite regions of the developing embryo, namely, *stem*, *leaf*, *root*, and *foot*. The upper anterior quadrant gives rise to the stem; the lower anterior develops into the first leaf; the lower

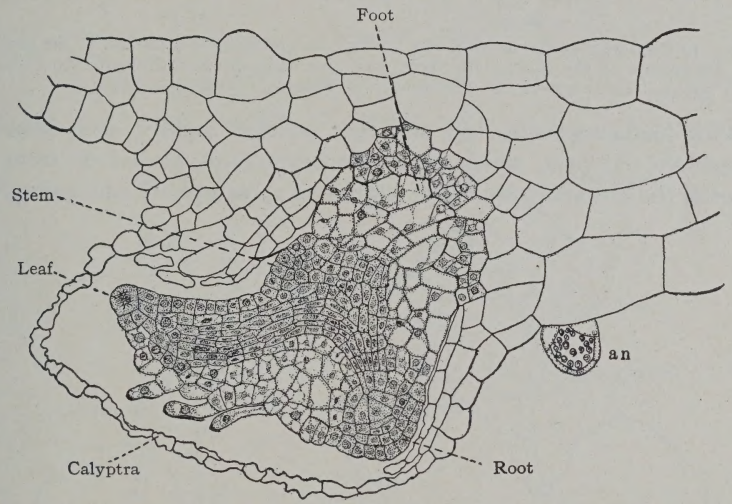


FIG. 361.—*Dryopteris mollis*. Longitudinal vertical section of gametophyte with a larger embryo sporophyte. The first leaf is about to break through the calyptra; the root is provided with a root cap; the large cells of the foot merge insensibly with the neighboring meristematic cells of the gametophyte, while the stem is relatively small.

posterior produces the first root; and the upper posterior becomes the foot. The subsequent cell divisions in each quarter are very regular at first, but the details will not be given here. As a result, however, we have a many-celled, globular embryo, in which the four original parts may be readily recognized in longitudinal vertical section, as shown in Fig. 360.

The region of the stem reveals the apical cell of that organ; the initial cells of the first leaf and of the root are also plainly shown.

As the embryo grows larger, these four regions develop at different rates, and the globular embryo soon takes the shape of a shoe (Fig. 361). At this stage, however, it is still enclosed in the calyptra. From this figure it is clear that the foot is a broad region whose cells merge gradually into those of the gametophyte. The leaf, ending in its apical cell, has

elongated appreciably. The apical cell of the root has given rise to the root cap. The stem develops at first more slowly than the other three regions.

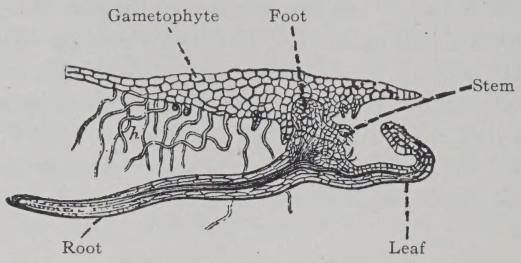


FIG. 362.—Longitudinal section of a young fern sporophyte attached to the gametophyte by means of the foot; root, stem, and leaf have broken through the calyptra. (From Sachs, "Lectures on the Physiology of Plants," Clarendon Press.)

With further growth, leaf and root develop rapidly, soon breaking through the calyptra, which, as in the bryophytes, is derived from the venter of the archegonium. The relation of gametophyte and sporophyte

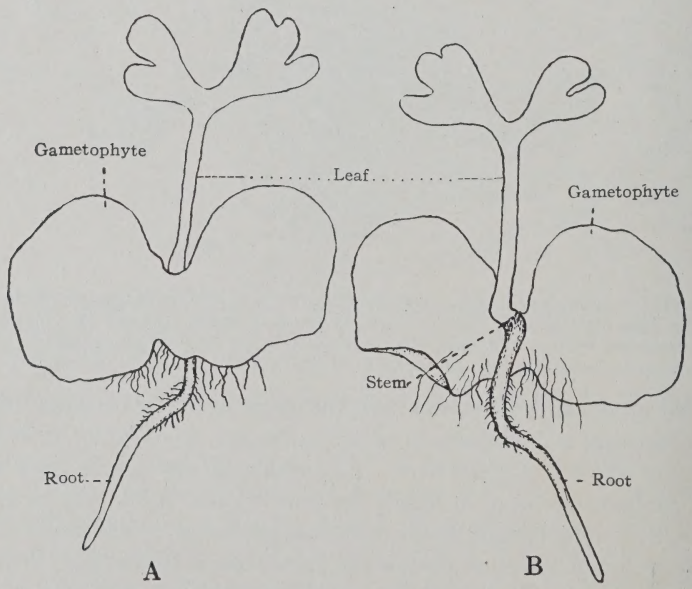


FIG. 363.—*Matteuccia nodulosa*. A, upper, and B, lower view of the same gametophyte with sporophyte attached.

is clearly brought out in a vertical section (Fig. 362). The leaf curves upward into the air through the notch of the prothallium, while the root strikes obliquely downward into the soil. The young sporophyte attached to the gametophyte is shown in Fig. 363, A, B. A is a view from above,

while B is the same specimen as seen from below. The stem is concealed behind the base of the leaf, and the foot is embedded in the gametophyte, posterior to the very short stem. In Fig. 364, A, we have a side view of the young fern dissected from the prothallium. The relation to one another of stem, leaf, root and foot is evident.

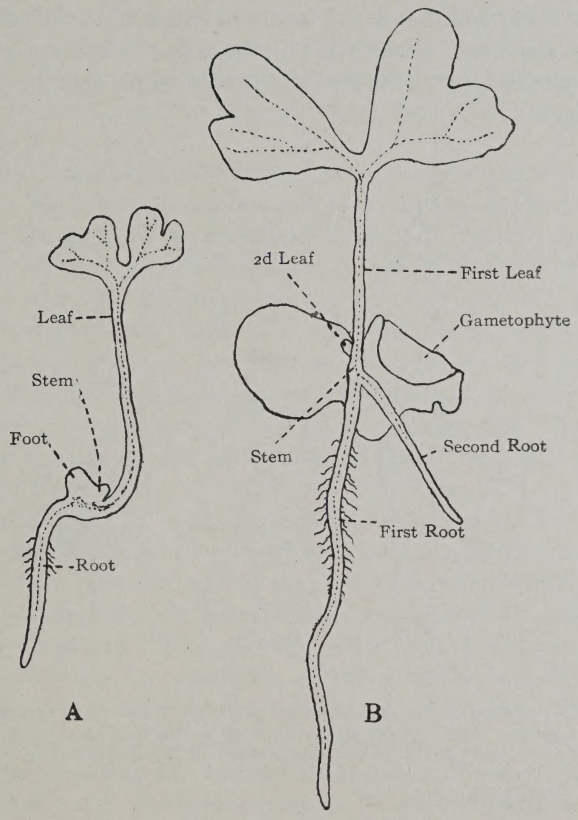


FIG. 364.—*Matteuccia nodulosa*. A, side view of young fern from which the gametophyte has been detached; primary vascular system indicated by a dotted line. B, an older plant, attached to prothallium, showing second root and beginning of second leaf.

Running through the center of leaf and root is the procambial strand (indicated by the dotted line) of elongated cells, the beginning of the vascular system of the young fern. The procambial strand which is differentiated later in the stem connects with this main strand of leaf and root. The stem is at first so small in comparison with leaf and root that the vascular system can be said to originate in leaf and root.

As the young fern continues its growth, additional leaves and roots appear. The first leaf, sometimes referred to as the *cotyledon*, never attains a large size. Each subsequent leaf, however, becomes larger than its predecessor, and the process continues until the adult size is attained. A similar course of development is followed in the roots. In the young fern shown in Fig. 364, B, the second root has grown out of the side of the short stem, and the second leaf is emerging from the end of the stem, which, in this view, is concealed by the base of the first leaf. The adult fern has already been described in a preceding paragraph, and illustrated in Fig. 350.

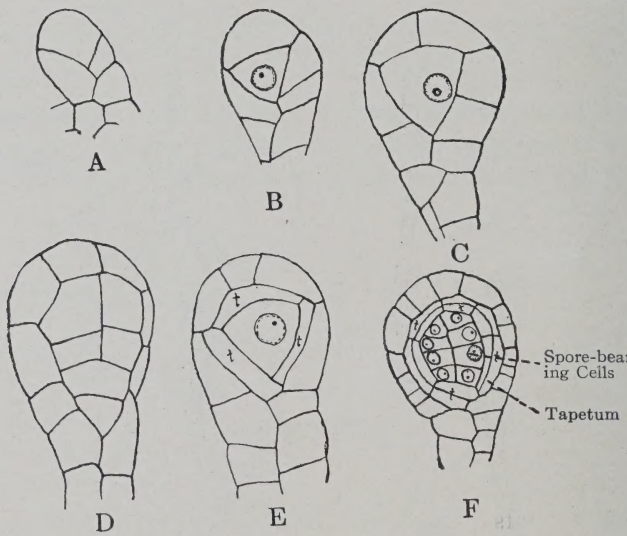


FIG. 365.—Stages in the development of the sporangium of *Polypodium falcatum*. A to F, successive stages in development from a single cell. D and E, surface and sectional views, respectively, of the same stage in development; *t*, tapetum. (From "Campbell's University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

Development of Sporangium and Spores.—In our ordinary ferns (Polypodiaceae) the sporangium originates from a single epidermal cell. Several early stages in the development are shown in Fig. 365, A to F. In the half-grown sporangium (F), there is differentiated a central mass of cells that will give rise to the spores. This central mass is surrounded by two layers of tabular cells constituting the tapetum, or nourishing cells (*t*). The wall of the sporangium is one cell thick, the row around the edge developing into the annulus. As the sporangium attains the mature size, the spore mother-cells round off and separate, the tapetal cells being changed into a liquid by digestion. Each spore mother-cell produces a

tetrad of four spores, as a result of two successive divisions of the nucleus and final cell divisions. The first nuclear division in the spore mother-cell is a reducing division. The spore possesses, therefore, the single number of chromosomes.

Vegetative Propagation of the Gametophyte.—If the life of fern prothallia be prolonged, vegetative propagation may be accomplished chiefly by the production of numerous lobes, or proliferations, which are separated by the death of older parts. In laboratory cultures, prothallia of certain ferns (Matteuccia, Osmunda) may branch dichotomously, and the branches may ultimately be separated by the dying away of older parts, as in the liverworts.

Vegetative Propagation of the Sporophyte.—A much greater variety of vegetative propagation is presented by the sporophyte. Here one of the most conspicuous kinds is the production of modified stems in the form of stolons, which take root and send up leaves. This is common in varieties of the Boston fern (*Nephrolepis exaltata*). In certain ferns (*Cystopteris bulbifera* (L) Bernh.) small bulbils are developed on the leaves. These fall off and may give rise to new plants. Another striking method is found in the Walking Fern (*Camptosorus rhizophyllus*), in which the tips of the leaves take root and produce new plants (see Fig. 75). New plants may arise also as adventitious buds from the fleshy roots of ferns, as in Ophioglossum.

Apogamy and Apospory.—Apogamy refers to the condition in which a sporophyte arises as a vegetative outgrowth from the gametophyte, and, of course, without the functioning of gametes. Of a considerable number of ferns in which apogamy is known to occur, may be cited two cliff brakes, *Pellaea atropurpurea* and *Pellaea glabella*, which grow on limestone ledges and escarpments. On the prothallia of these species, antheridia with normal sperms are regularly developed, but no archegonia. The sporophyte arises as an outgrowth from the anterior part of the archegonial cushion (midrib).

On the other hand, the term, *apospory*, is applied to the origin of gametophytes from the sporophyte without the functioning of spores. In certain ferns, which are aposporous, if the leaf blades be fastened against the surface of the soil, prothallia bearing sex organs and functional gametes will develop, generally from spots on the leaf which would normally produce sporangia.

Classification of the Pteridophytes

The Pteridophyta may be divided into three great classes: *Filicinae*, ferns and their allies; *Equisetinae*, horsetails and scouring rushes; and *Lycopodinae*, club mosses.

Although gametophyte and sporophyte in these great classes may differ widely in habit, structure, and adaptation to environment, the life history, when traced from spore to spore, is fundamentally the same as that given in the preceding pages for a commonly known fern. The following classification is intended as an abbreviated outline:

Class 1. Filicinae. Ferns and fern-like plants

Subclass 1. Eusporangiate ferns. Sporangia without an annulus, opening vertically by two valves. In development the whole sporangium is not readily traced back to a single epidermal cell. All are homosporous.

Family: Ophioglossaceae. Leaves not rolled up in the bud like a watch spring.

Ophioglossum, Adder's Tongue Fern.
Botrychium, Moonwort, Rattlesnake Fern.

Family: Marattiaceae. Sporangia without an annulus. All Tropical.
Marattia, Angiopteris, &c.

Subclass 2. Leptosporangiate ferns (Filices). Sporangium arising from a single epidermal cell.

(*a*) Homosporous. Spores of one kind.

Family: Osmundaceae. Sporangia with rudimentary annulus; opening vertically. Osmunda, Interrupted Fern, Cinnamon Fern, Royal Fern.

Family: Polypodiaceae. Sporangia with complete annulus.

Matteuccia, Ostrich Fern.
Onoclea, Grape Fern, Sensitive Fern.
Adiantum, Maidenhair Fern.
Pteris (Pteridium), Brake Fern.
Dryopteris, Shield Fern, Christmas Fern.
Asplenium, Spleenwort.
Polypodium, Polypody.
Camptosorus, Walking Fern.

(*b*) Heterosporous. Spores of two kinds, microspores and megaspores, producing respectively male and female gametophytes.

Family: Marsiliaceae, Pepperworts.
Marsilia, Pilularia.

Family: Salviniaceae. Azolla, Salvinia.

Class 2. Equisetinae. Horsetails

Equisetum.

Class 3. Lycopodinae. Club Mosses

Family: Lycopodiaceae.
Lycopodium. Club Mosses
Family: Psilotaceae.
Family: Selaginellaceae.
Selaginella.
Family: Isoetaceae.
Isoetes. Quillwort.

Ophioglossaceae.—This family is represented in our flora by two genera, Ophioglossum and Botrychium. Species of both genera are rapidly approaching extinction, owing to the disappearance of the native woodlands.

Ophioglossum is a small fern with a short, upright underground stem, bearing fleshy roots, and sending up each year a single leaf. At the side of the base of the naked leaf stalk is the bud (Fig. 366, A). In spore-bearing specimens, the leaf has a vegetative and a spore-bearing segment. The sporangia are completely embedded, and open by a transverse slit (B). The sporophyte is propagated vegetatively from the fleshy roots.

The gametophyte in both Ophioglossum and Botrychium is a small, dark brown, tuber-like, subterranean body, irregular in form, and about one to one and a half centimeters or more in length (Fig. 367, A, B). It is destitute of chlorophyll. The cells of the ventral part contain an endophytic fungus, which doubtless assists the plant in securing nourishment from the soil. The relation between the gametophyte and the fungus is probably one of mutual symbiosis. The sex organs are developed chiefly on the dorsal side, the antheridia being confined largely to the dorsal ridge, and the archegonia to the slopes (Fig. 367, A). The antheridia are deep-seated.

In Botrychium the leaf requires three or more years to reach maturity. The base of the leaf forms a sheath which completely encloses the apex of the stem and the bud. In spore-bearing specimens, the leaf has also two segments, both much branched, the spore-bearing and the foliage (Fig. 366, C, D). In Fig. 367, B, is shown a young sporophyte still attached to its gametophyte.

Marattiaceae.—The Marattiaceae include a small number of tropical species, which, in general appearance, resemble ordinary ferns. In temperate climates they are cultivated in large conservatories along with large tree ferns (Cyatheaceae) and other exotics. In Marattia and Angiopteris the stem is a thick, stocky, tuber-like structure, which may attain a diameter of half a meter, with a crown of leaves that may reach a length of four or more meters. The leaves are circinate in the bud.

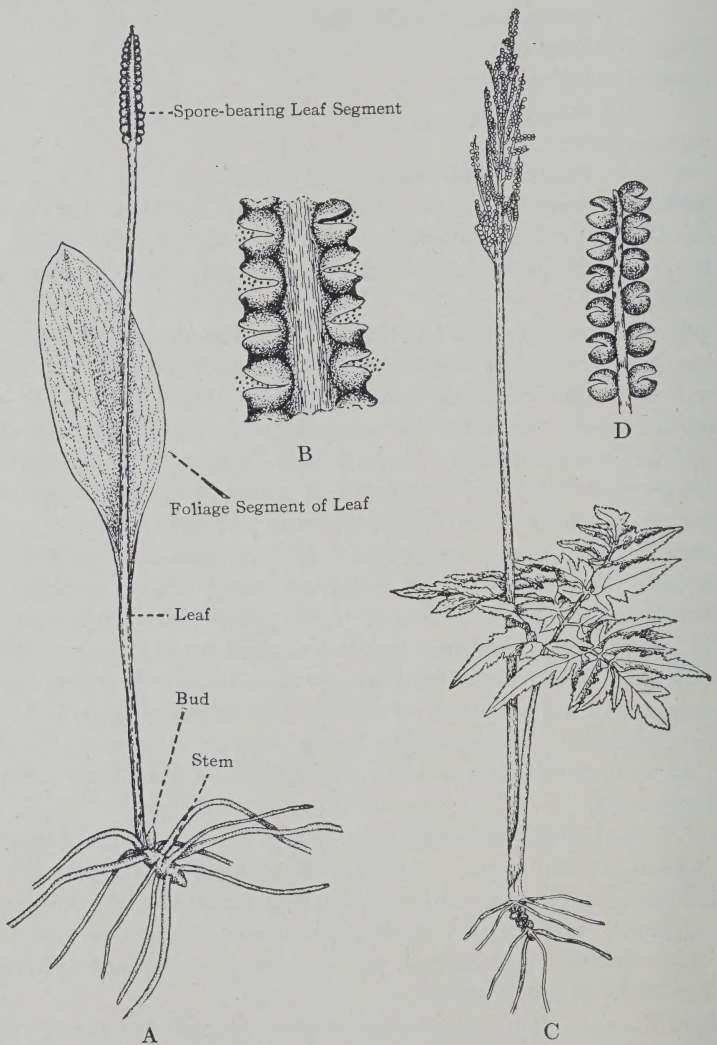


FIG. 366.—A, *Ophioglossum vulgatum*. B, portion of spore-bearing segment of leaf. C, *Botrychium obliquum*. Whole plant reduced in size. D, spore-bearing pinna with open sporangia, enlarged.

The sporangia, which are borne on the foliage leaves, are united into masses known as *synangia*, in which the individual sporangia are not always clearly recognized. The sporangia do not have a ring, but open by a longitudinal slit.

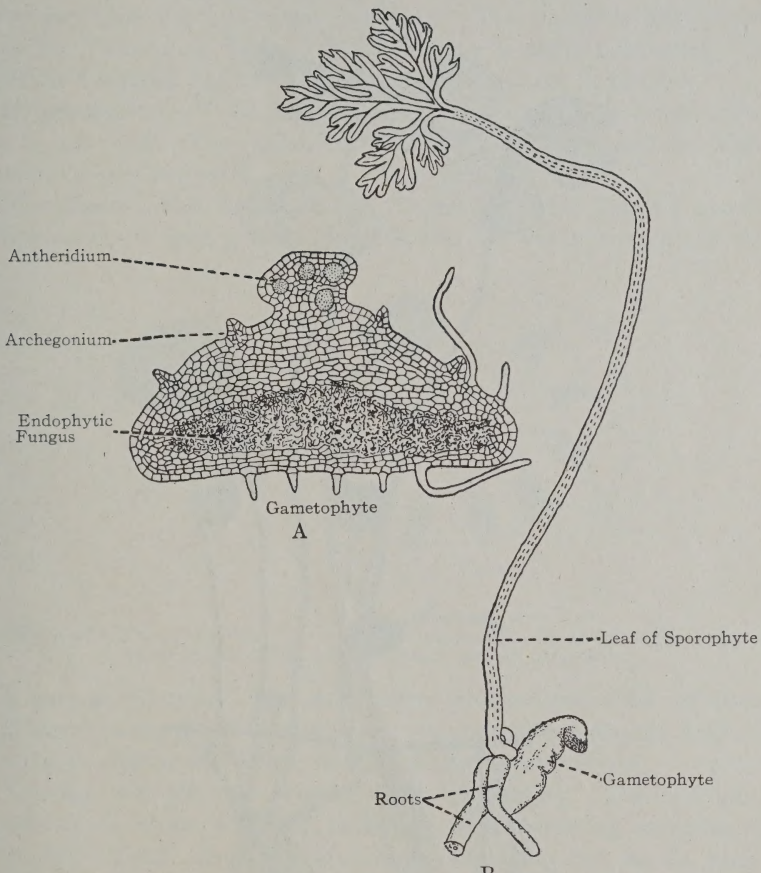


FIG. 367.—*Botrychium virginianum*. A, transverse section of gametophyte; antheridial ridge with imbedded antheridia. B, gametophyte with young sporophyte attached. (A, from Jeffrey; B, from Campbell's "University Text-Book of Botany." By permission of the Macmillan Company, Publishers.)

The gametophyte is a fleshy, green thallus, resembling a small liverwort in appearance. It is monoecious, and both sex organs are borne on the under side. Endophytic fungi are present in some species.

Osmundaceae.—The Osmundaceae are large, handsome ferns often found in wet or marshy places, where they form large tussock-like clumps. The tall, graceful leaves, once or twice pinnate, may attain a length of

two meters. When young the leaves are clothed with a loose, light-colored wool. In *Osmunda claytoniana* L. the sporangia are restricted to two to five pinnae near the middle of certain of the leaves. These pinnae

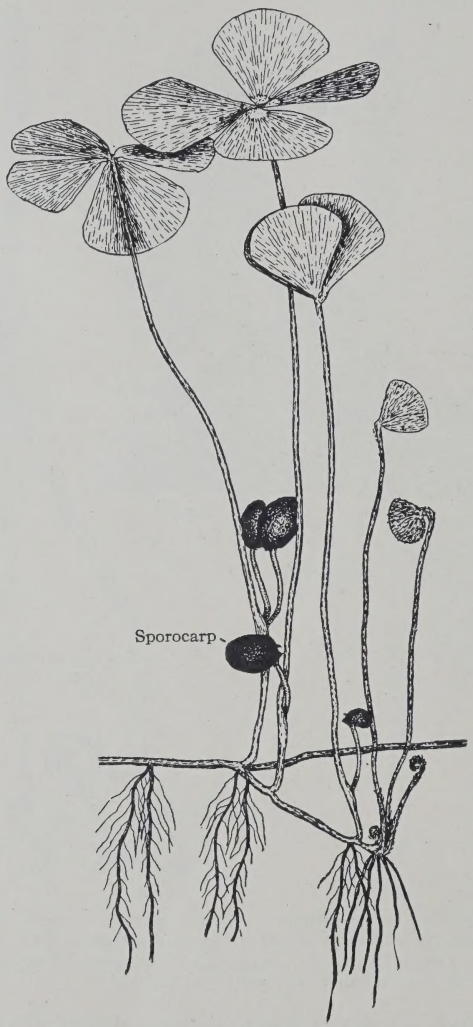


FIG. 368.—*Marsilia quadrifolia.* Habit of sporophyte.

are completely transformed into spore-bearing structures. In *Osmunda cinnamomea* L., commonly known as the Cinnamon Fern, the leaves are of two kinds, foliage and spore-bearing. The spore-bearing leaves appear first in the season, but they soon wither and disappear after the

spores are shed. The rusty-brown wool covering the leaves when young, together with the brown, shriveled sporangia, give these structures a decided cinnamon color. *Osmunda regalis* L. is cosmopolitan in distribution. The spore-bearing leaflets are confined to the summit of the leaf, where they form a sort of racemose panicle. This species is often referred to as the "Flowering Fern." *O. claytoniana* is easily cultivated. The species of Osmunda are in danger of becoming extinct in Indiana.

Polypodiaceae.—These include the vast majority of the common ferns now in existence. They often occur in great numbers, and are widely distributed over the earth.

Marsiliaceae and Salviniaceae.—These are either floating aquatics (Salviniaceae) or they grow in localities that are wet or swampy, at least

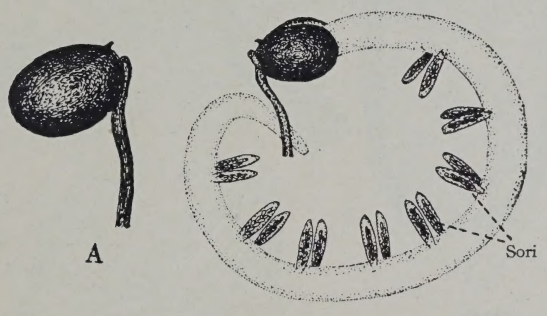


FIG. 369.—*Marsilia quadrifolia*. A, sporocarp (enlarged). B, germinating sporocarp, showing gelatinous cord, to which sori are attached.

for a part of the year. The sporophytes produce two kinds of spores: small microspores, which give rise only to male gametophytes, and relatively large megaspores which produce female gametophytes.

Marsilia will serve to illustrate the life history. The sporophyte consists of a slender, creeping, branched stem consisting of nodes and internodes. From the nodes arise numerous roots and leaves, each of the latter having four small triangular leaflets, which give the plant the appearance of a tuft of four-leaved clover (Fig. 368). The spores are borne on modified leaf segments termed *sporocarps*. The sporocarp, which has a hard shell, resembles a small, flat bean. Within the sporocarp of Marsilia both microsporangia and megasporangia are developed in clusters, sori. Only one megaspore is fully developed in a megasporangium, while the microsporangium produces a large number of microspores. In volume a megaspore is several hundred times as large as a microspore. The difference in size is shown in Fig. 370, A and B, which were drawn to the same scale.

A short time after the sporocarps are placed in water, especially if a small opening has been made in the shell, the entire contents will escape in the form of a colorless, gelatinous cord bearing two rows of sori, each sorus containing both kinds of spores (Fig. 369, B). With the exception of the spores, the entire cellular structure within the hard wall of the sporocarp is converted into the colorless jelly.

The Microgametophyte.—The microspore has a wall of three layers, the outer layer being very thick and composed of small, prismatic rods

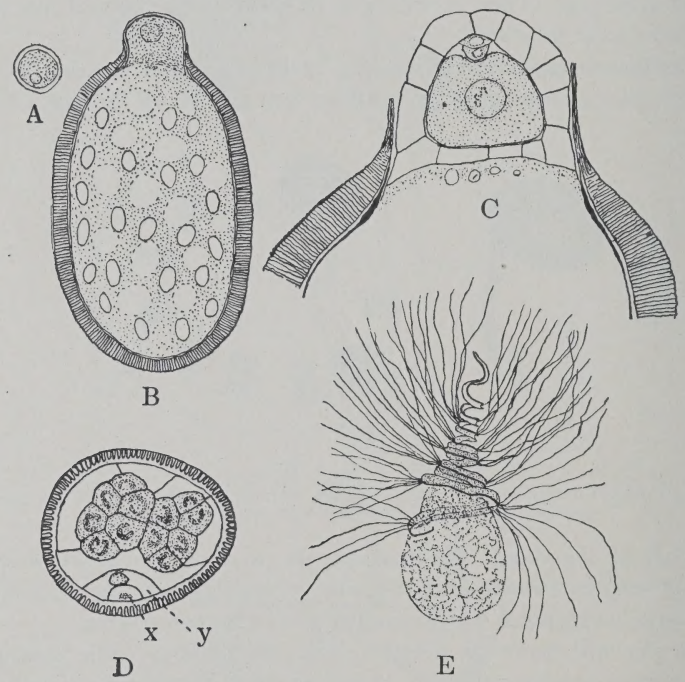


FIG. 370.—*Marsilia quadrifolia.* A, B, microspore and megaspore, drawn to the same scale. C, upper end of megaspore with the megagametophyte consisting of an archegonium only. D, microspore, containing microgametophyte (×400); *x*, *y*, vegetative prothallial cells; the sperm-bearing cells are shaded. E, a sperm, highly magnified. (C, D, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

The microgametophyte is very small, merely filling the cavity of the spore. It develops with great rapidity, reaching maturity in fifteen or twenty hours after the spore begins to germinate. It consists of two vegetative cells (Fig. 370, D, *x*, *y*) and an antheridium bearing two masses of sperms. The two masses of spermogenous cells have been regarded as representing two antheridia. The sperms are shaped like a corkscrew, having a dozen or more turns, and bearing many cilia (Fig. 370, E).

The Megagametophyte.—The megaspore is an ellipsoidal cell, about .4 by .7 mm. in diameter, ivory-white in color, and provided with a very thick wall. Like that of the microspore, the wall consists of three layers, the outer being thicker and prismatic in structure (Fig. 370, B). At one end of the spore there is a rounded protuberance, in which lie the nucleus and the bulk of the cytoplasm. The thick prismatic layer of the cell wall does not cover this protuberance. The cavity of the spore is rich in food material, composed chiefly of starch and protein. The megagametophyte,

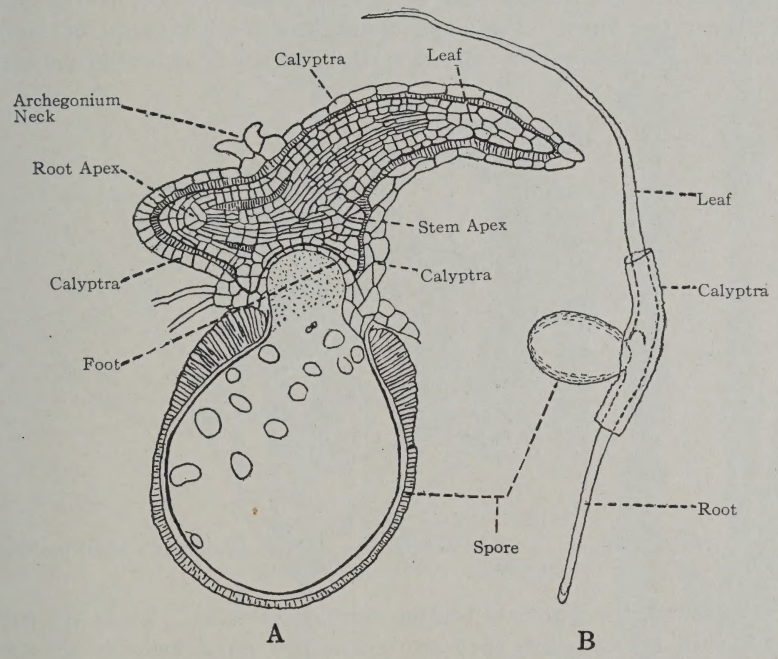


FIG. 371.—Marsilia and Pilularia. A, embryo of Pilularia still enclosed within the calyptra. B, young sporophyte of Marsilia still attached to spore and partly enclosed in the calyptra × 12. (A, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

like the microgametophyte, is reduced to its lowest terms, consisting merely of an archegonium with a very short neck (C).

In neither micro- nor megagametophyte do the primordia of the chloroplasts develop chlorophyll unless the life of the gametophytes is prolonged. Sometimes, however, the megagametophyte will send out rhizoids, and chlorophyll will be developed to a limited extent.

The development of the embryo is very similar to that in a polypodiaceous fern. Fig. 371, A, is a median longitudinal section of an embryo sporophyte of Pilularia still attached to the spore and enclosed within the

gametophyte. In B is shown the young sporophyte of Marsilia, in which the first root and leaf have broken through the calyptra. The whole bears a striking resemblance to the seedling of certain seed-bearing plants.

Salviniaceae.—The two genera, Salvinia and Azolla, are small floating aquatics. Azolla occurs in the southern states, developing in large quantities on the surface of quiet stretches of water. It occurs also in California. European species of Salvinia occur also in a few places in the United States. The slender stem in Salvinia is concealed by the leaves, which are of two kinds. The larger, dorsal leaves, a centimeter or more in diameter, are arranged in two rows; the two rows of ventral leaves are

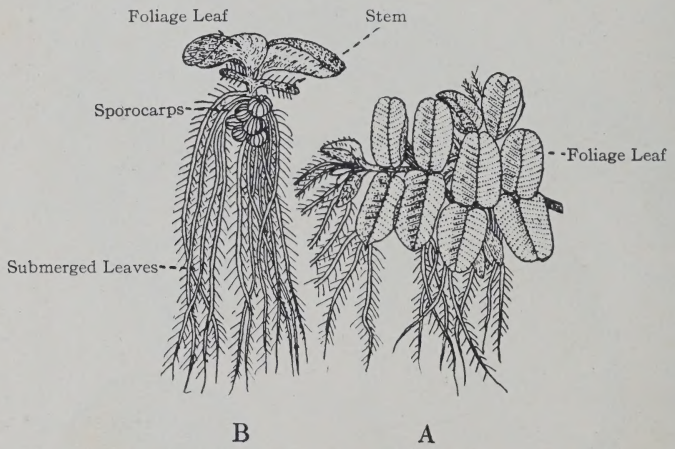


FIG. 372.—*Salvinia natans*. A, plant as seen from above. B, part of a plant bearing sporocarps. (From Pringsheim.)

finely dissected, the segments bearing rhizoid-like hairs. Roots are not developed in Salvinia, but they are represented physiologically by the dissected ventral leaves (Fig. 372, B). The leaves of Azolla are in two dorsal rows. They are very small and moss-like. Roots are present in Azolla. Rounded sporocarps are developed in both Salvinia and Azolla, those of the one differing considerably from those of the other, and from that of Marsilia. The gametophytes are greatly reduced, being similar in character to the gametophytes of Marsilia.

CLASS II. EQUISETINAE

The living representatives of the second class of Pteridophytes, the Equisetinae, are included in the one genus, Equisetum, of which there are about twenty-four species. Fourteen of these are said to occur in the United States.

FIG. 373.—*Equisetum arvense*. A, underground rhizome with spore-bearing shoots B, terminating in cones (flowers) of sporophylls; *b*, the axis of the cone has elongated permitting the sporophylls to be separated and the sporangia to open; *a*, tuber. C, a foliage shoot. (After Wossidlo.)

Sporophyte.—The outstanding characteristic of the sporophyte, by which it is distinguished from the ferns, lies in the fact that the hollow shoots are jointed, and the rudimentary leaves appear as toothed sheaths at the joints (Fig. 373, A). The sporophylls form a cone at the apex of the shoots, and the spores are provided with hygroscopic appendages, the elaters (Fig. 374, C, D, E).

The main stem is an underground rhizome, showing the same differentiation into nodes and internodes as its aerial branches (A, B). From each node of the rhizome, which bears a sheath of leaves, arise the roots, branches, and aerial shoots. At the nodes rounded tubers, which may remain dormant or develop roots and shoots are not infrequently formed.

In some species, as in *Equisetum arvense*, two sets of aerial shoots are developed, spore-bearing and foilage shoots. The spore-bearing shoots (B), which appear in early spring, are colorless or reddish brown in color, little or no chlorophyll being developed. After the spores are shed, these

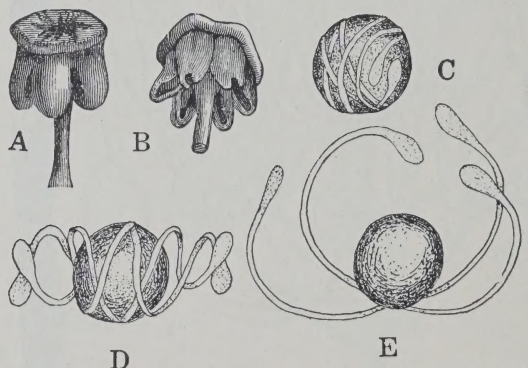


FIG. 374.—*Equisetum arvense*. A, sporophyll seen from the side. B, sporophyll seen obliquely from below. C, spore with the spiral bands of the perinium (elaters). D, the elaters are separating. E, a dry spore. (After Wossidlo.)

shoots wither and disappear. As the spore-bearing shoots vanish, the foilage shoots (C) begin to appear above the ground. The latter are green and much branched. When about mature they present the appearance of a well groomed horse's tail, especially when they are held in an inverted position. The leaves of these shoots are reduced to small teeth, forming a sheath at each joint. The photosnythetic work of the plant is performed mainly by the tissues of the stem. Such stems are termed *cladodia*.

In other species, such as *E. hyemale* and *E. laevigatum*, only one kind of aerial stem is developed. These are reed-like and may be branched or unbranched, the spore-bearing branches ending in a cone (Fig. 375). Owing to the large quantity of silica in the cell walls, these reed-like stems

were gathered in colonial days and used in scouring metal vessels,—hence the name, *scouring rush.*

The Sporophylls.—The sporophylls are umbrella-shaped and arranged in close circles at the ends of the shoots, forming a cone (Fig. 373, B, *b*). The blades of the sporophyll, because of mutual pressure, are usually hexagonal. At the edge, on the under side of the hexagonal blade, are a number of pendent, sac-like sporangia. Each sporangium opens by a longitudinal slit on the inner side (Fig. 374, A, B). When the spores are mature the axis of the cone elongates, thus freeing the sporophylls and permitting the spores to fall out (Fig. 373, B, *b*).

The outer coat of the spore is split into four strips, which, when moist, are coiled around the cell (Fig. 374, C). When dry they straighten out somewhat and appear as four strips attached to the spore (D, E). The adaptive function of these so-called *elaters* seems to be to insure the dispersal of the spores in groups. When the sporangium opens, the elaters tend to become entangled, with the result that the spores fall out in clusters, and, in that form, may be blown about by the wind. The result is that several spores may be deposited close to one another, and, since the gametophytes are usually dioecious, the probability of fecundation being accomplished is greater than were the male and female prothallia removed from one another by considerable distances.

FIG. 375.—*Equisetum hyemale.* Distal end of aerial branch ending in a cone.

Structure of the Stem.—The shoots of Equisetum are very porous in structure, the vascular system being scantily developed. Running lengthwise in the internodes are a large central cavity in the pith, a circle of similar cavities in the cortex, and one in each vascular bundle. These cavities are formed by the disorganization of the tissues. The vascular bundle is reduced to a few protoxylem elements and a few sieve elements. A diagram of a cross section of the spore-bearing shoot of *Equisetum arvense* is shown in Fig. 376. Fig. 377 is a cross section of a vascular bundle with its large water passage.

The Gametophyte.—The gametophyte of Equisetum is a somewhat flattened, irregularly branched or lobed, green structure resembling, in general, certain fern prothallia or the gametophytes of certain liverworts (Fig. 378). The gametophyte is generally dioecious. The male plants are often smaller, and the antheridia develop earlier than the archegonia.

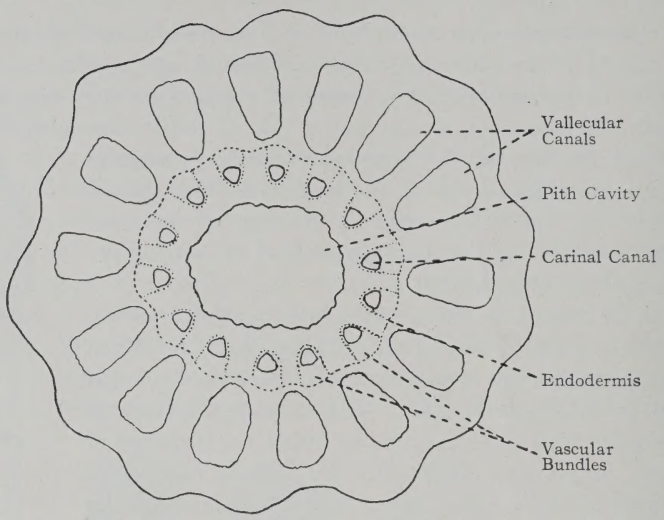


FIG. 376.—*Equisetum arvense.* Diagram of a cross section of an internode of a spore-bearing shoot; carinal canals are water passages.

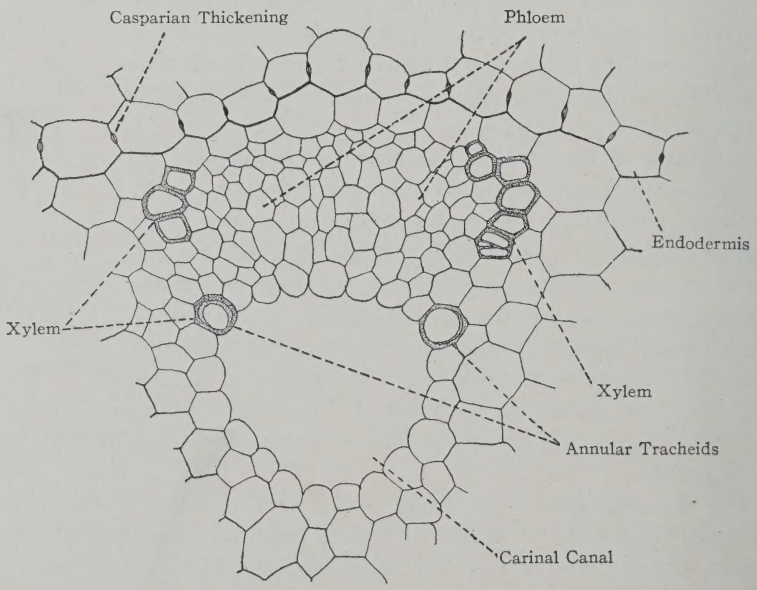


FIG. 377.—*Equisetum arvense.* Cross section of vascular bundle of spore-bearing shoot.

The antheridia and archegonia bear a close resemblance to those organs in the eusporangiate ferns.

Class III. Lycopodinae. Club Mosses

The typical Club Mosses are readily distinguished from the other Pteridophyta, especially the ferns, by the moss-like appearance of the sporophytes, which possess small, moss-like leaves that thickly clothe the young stem.

The living representatives comprise four families: Lycopodiaceae, Psilotaceae, Selaginellaceae, and Isoetaceae, although there are valid reasons for placing the last named family in a class by itself.

Lycopodiaceae.—The sporophyte of Lycopodium consists chiefly of an upright stem, as in *L. lucidulum* (Fig. 379), or a slender, creeping

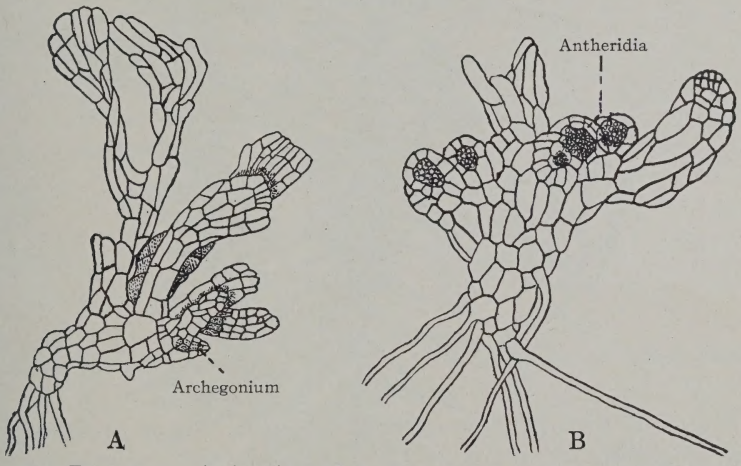


Fig. 378.—Equisetum. A, female, and B, male, gametophytes. (From Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

rhizome, from which spring upright branches, as in *L. clavatum* or *L. complanatum* (Fig. 381). Branching is either monopodial or dichotomous. The leaves are very simple in structure, and are traversed by a single median vascular bundle. The roots may branch dichotomously. In some species the sporophyte is propagated vegetatively by small leafy buds (gemmae), which fall off and grow into separate plants (Fig. 379, A, B, C).

Sporangia.—The sporangia are somewhat kidney-shaped, and borne singly on the adaxial side of the sporophylls, which may differ very little from the regular foliage leaves, as in *L. lucidulum* (Fig. 380). In certain species the sporophylls are closely aggregated in cones (strobili) borne at the ends of upright shoots (Fig. 381). The spores are of one kind.

The Gametophyte.—In certain species the gametophyte is a small, flattened, tuber-like structure similar to that of Botrychium, growing

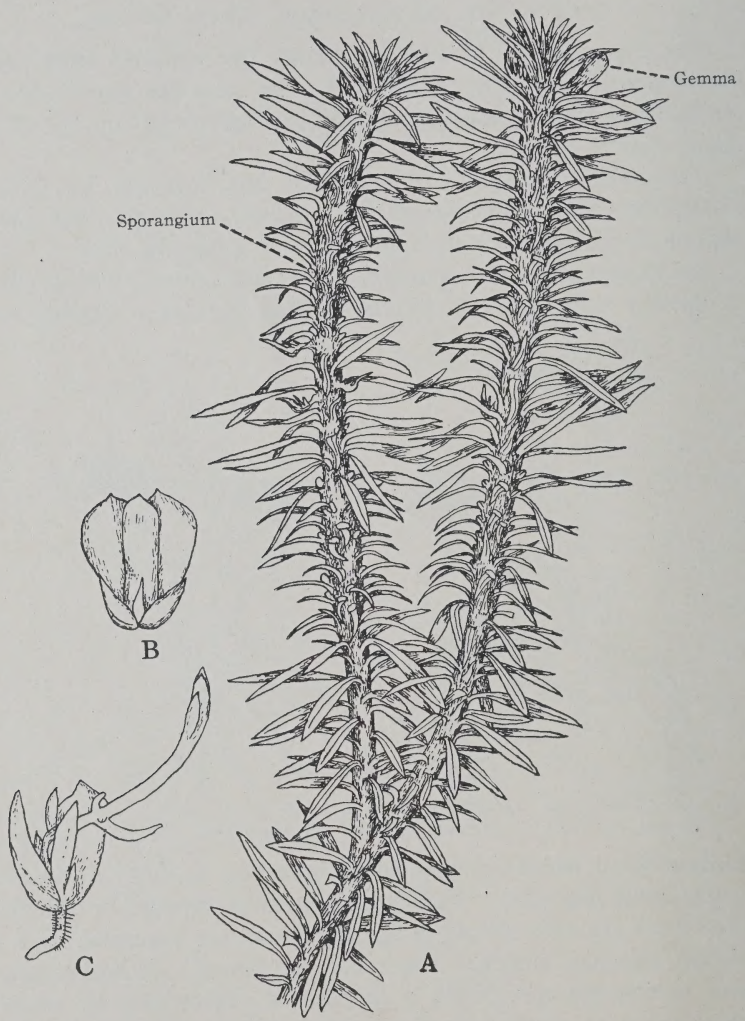


FIG. 379.—A, Sporophyte of *Lycopodium lucidulum* Michx. B, Gemma, or bud ×4. C, young plant of *Lycopodium selago* arising from germinating bud. ×4. (B, from Cramer. C, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

saprophytically beneath the surface of the ground, as in *L. annotinum* (Fig. 382). In other species, as in *L. complanatum*, the gametophyte is

an upright, somewhat cylindrical body terminating in a crown of leaf-like lobes containing chlorophyll, in which the sex organs are located (Fig. 383, A, B). Chlorophyll is not developed in the underground portion. In cells of a definite region an endophytic fungus occurs, which assists the gametophyte in securing nourishment from the soil.

As stated, the sex organs are borne on the crown or on the upper side. The antheridia are more massive than in the ferns, resembling those of Equisetum or of the Ophioglossaceae. The archegonia are also larger than those of the fern, bearing a strong resemblance to those of the liverworts.

In the development of the young sporophyte in a certain species, a small, tuber-like stem, called a *protocorm*, is first formed. From it the

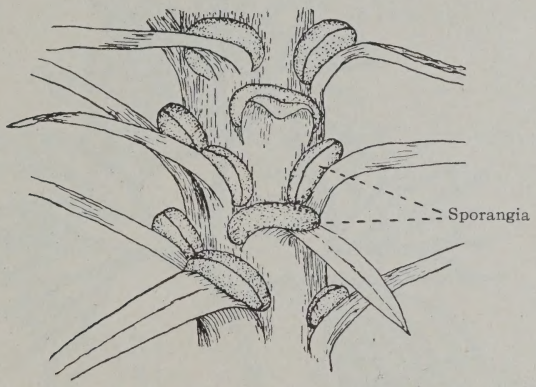


FIG. 380.—*Lycopodium lucidulum* Michx. Portion of stem enlarged, showing position of sporangia.

roots and stem later develop. Several sporophytes may be formed on one gametophyte. The gametophyte shown in Fig. 382 bears two visible sporophytes, one larger than the other. The development of the young sporophyte is slow, being dependent upon the gametophyte for a long time.

Phylloglossum.—The one species, *Phylloglossum drummondii*, native to Australia, is a small plant resembling a young sporophyte of Lycopodium (Fig. 384). The spores are borne in a small strobilus at the end of a short, naked stalk.

Psilotaceae.—This is a small family of plants, mostly tropical. One species (*Psilotum triquetrum*) is found in Florida. The sporophyte is usually epiphytic. It is a slender, creeping, leafless stem. The roots, which develop from rhizome-like shoots, branch dichotomously. Specimens are sometimes cultivated in large conservatories along with other exotic plants.

Selaginellaceae.—The sporophyte of Selaginella bears a close resemblance to that of certain species of Lycopodium. In some species the

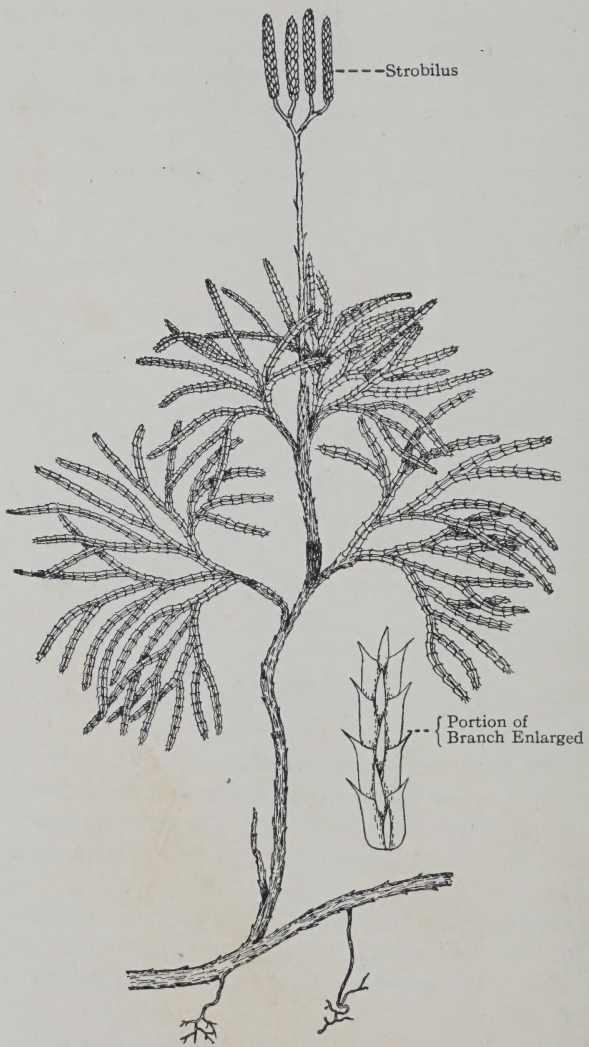


FIG. 381.—Portion of the sporophyte of *Lycopodium complanatum flabelliforme* Fernald. A portion of branch is enlarged to show arrangement of leaves.

leaves are all alike (as in *S. arenicola* Underw.), and arranged spirally on the stem; while in others they are arranged in four rows, two rows of large leaves and two of small ones, as in *S. kraussiana* (Fig. 387). A

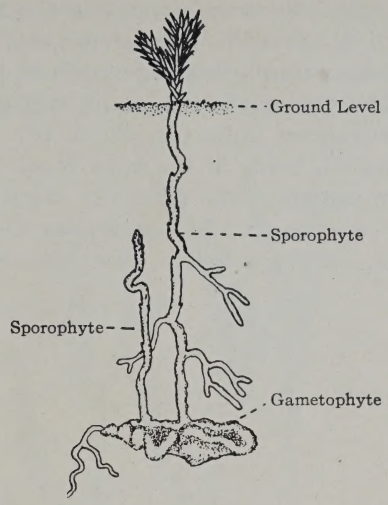


FIG. 382.—*Lycopodium annotinum.* The flattened gametophyte, bearing two sporophytes. (From Bruchmann.)

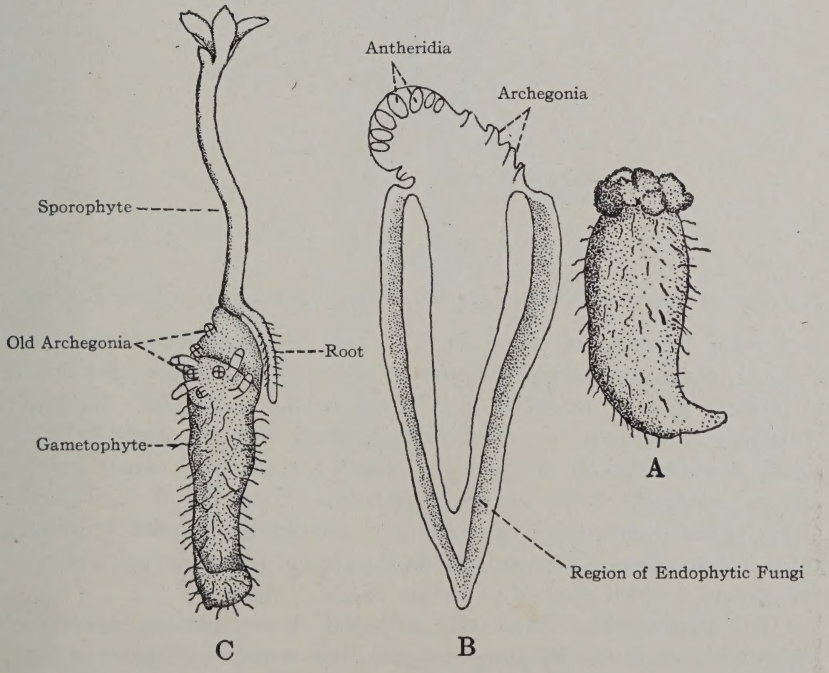


FIG. 383.—Gametophytes and young sporophyte of Lycopodium. A, B, tuberous gametophyte of *L. complanatum;* B, in longitudinal section; the shaded region indicates the location of the endophytic fungus. C, *L. lucidulum.* (A, from Bruchmann; B, C, from Spessard.)

characteristic of Selaginella is the development of a small outgrowth at the base of the leaf on the adaxial side, known as a ligule.

Selaginella differs markedly from Lycopodium, however, in that it is heterosporous. The sporophylls are usually aggregated in cones borne at the ends of the branches (Figs. 385, 386, A, B). Both microsporangia and megasporangia are borne in the same cone. Sporangia are borne singly on the stem just above the leaf axils. Each sporophyll subtends, therefore, but one sporangium. In most species the lower sporangia bear the megaspores, four to a sporangium, while those higher in the strobilus

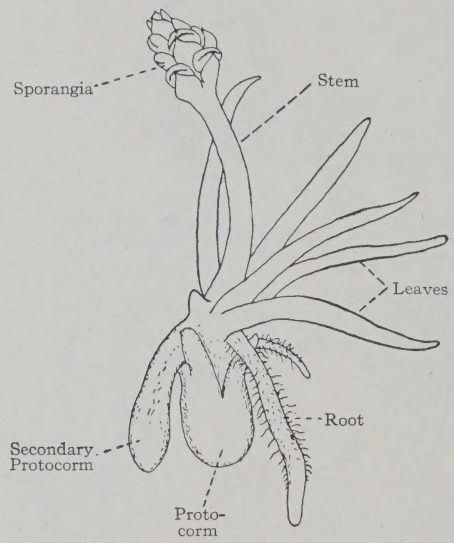


FIG. 384.—A plant of *Phylloglossum drummondii*, × about 3. (From Bertrand.)

bear many microspores (Fig. 386, B). The vast majority of species are tropical, but a few occur in temperate regions. *Selaginella apus* occurs in Indiana, growing on moist earth along the shores of lakes. As a rule they have a profusely branched, creeping stem, forming moss-like mats; some, however, climb on adjacent plants and develop stems several meters in length. Some species grow erect. Those like *S. lepidophylla* and *S. rupestris*, growing in dry situations, are capable of resisting drought for many months. These are among the specimens known as "resurrection plants," which are sold in certain curiosity shops.

The Gametophyte.—The plants being heterosporous, there are naturally two kinds of gametophytes, the male, microgametophyte, developing from the microspore, and the female, megagametophyte, produced by the megaspore.

The microgametophyte is very small, merely filling the cavity of the spore, and resembling that of Marsilia (Fig. 388, A). It consists of a central mass of sperm-bearing cells surrounded by a single layer of cells

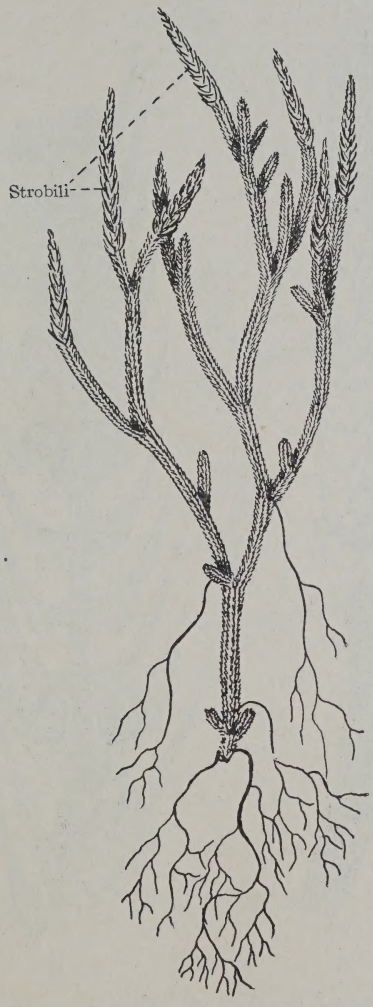


FIG. 385.—*Selaginella arenicola* Underw. Habit of sporophyte.

which finally break down, liberating the sperms. Chlorophyll is not developed. In reality the microgametophyte seems to consist of a single antheridium and a vegetative cell, or so-called *prothallial cell*. The sperms are biciliate.

The megagametophyte is also largely confined to the megaspore, protruding only slightly, when mature, through an opening in the thick spore wall. Chlorophyll is not developed at all, or only to a very limited

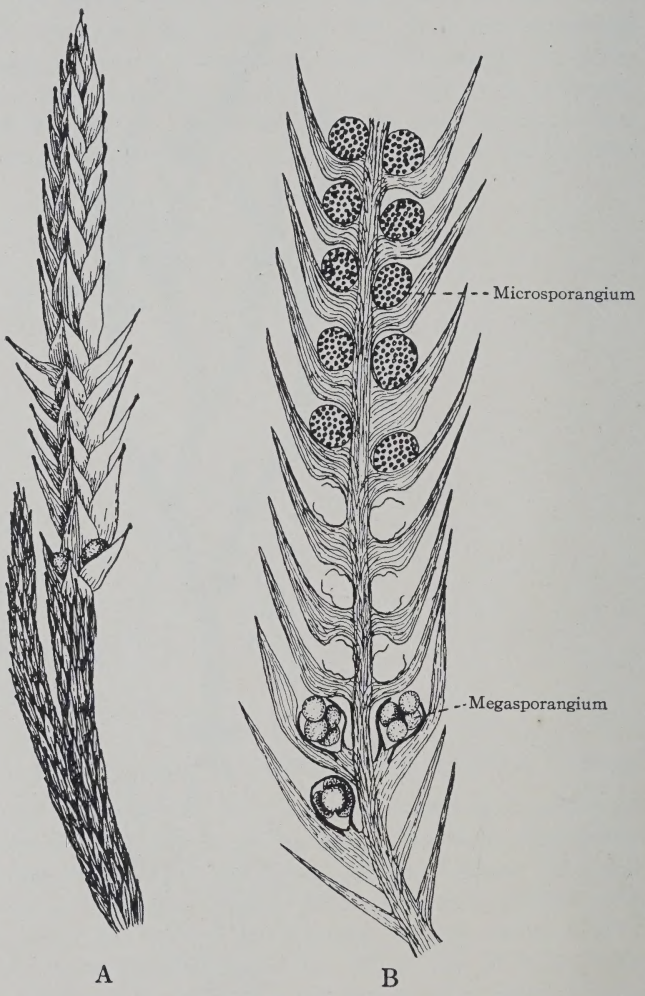


FIG. 386.—*Selaginella arenicola* Underw. A, end of a branch with a spore-bearing cone, much enlarged. B, longitudinal section of cone.

degree in that portion protruding from the spore (Fig. 388, C). In both micro- and megaspores sufficient food is stored for the complete development of the gametophytes, and, in the case of the megaspore, for the early development of the embryo sporophyte as well.

Fig. 389, A represents a section through a megagametophyte enclosing two embryo sporophytes. As in the case of the fern, the embryo, while

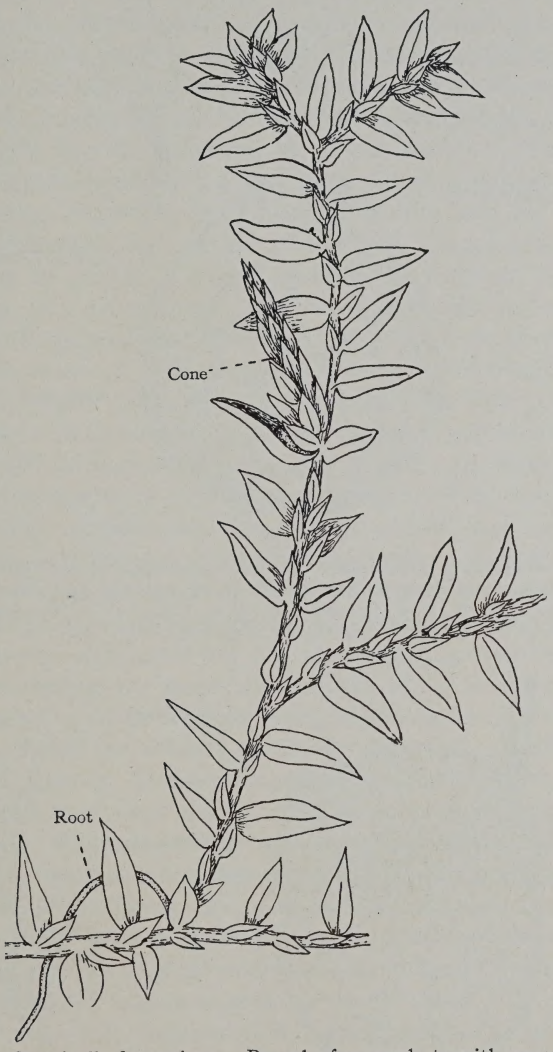


Fig. 387.—*Selaginella kraussiana.* Branch of sporophyte with spore-bearing cone. (From Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

enclosed in the gametophyte, shows the three distinct regions, foot, root, and stem. The stem at the stage in question shows the beginning of two young leaves; each will bear a ligule at its base. There is an additional

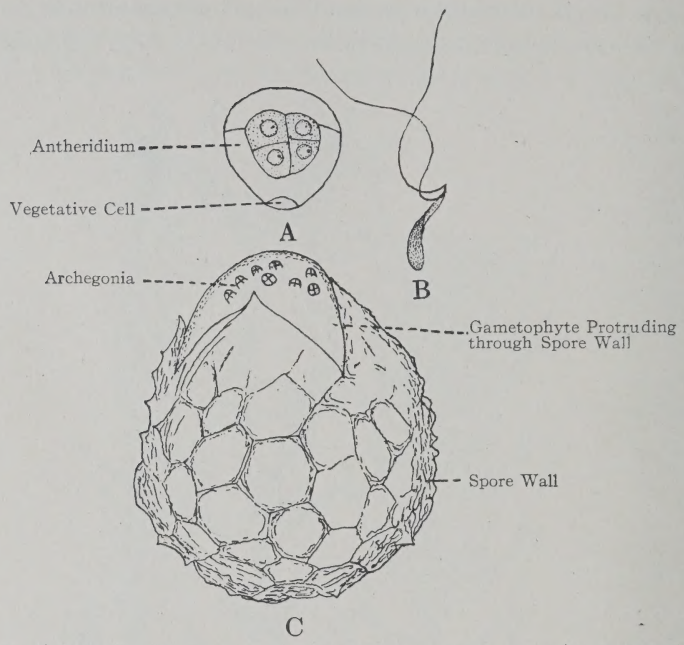


FIG. 388.—*Selaginella kraussiana.* A, microgametophyte not quite mature. B, sperm. C, megagametophyte within the old spore wall, the protruding part bearing the archegonia. (A, B, from Belajeff. C, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

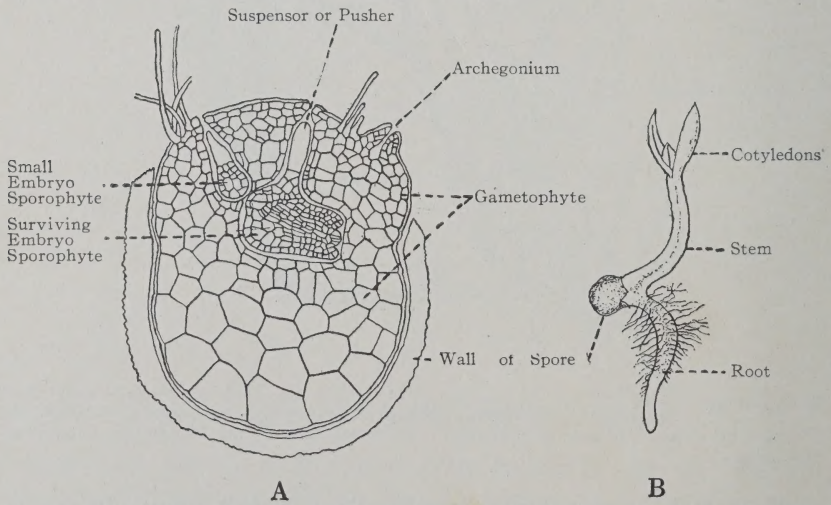


FIG. 389.—Selaginella. A, *Selaginella martensii;* vertical section of megagametophyte, with two embryo sporophytes, partly enclosed by the wall of the megaspore. B, *S. kraussiana;* young sporophyte still attached to the spore. (A, adapted from Strasburger, after Pfeffer. B, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

organ not present in the embryo of the ordinary ferns, but present in some of the Ophioglossaceae, namely, the "suspensor" (Fig. 389, A), or in reality the *pusher*. As in Lycopodium, the suspensor is the first part of the embryo to be differentiated, and it seems to push that part from which foot, stem and root develop, down into the tissue of the gametophyte. We have here, therefore, a tolerably well differentiated embryo sporophyte completely surrounded by the tissues of the gametophyte. More than one sporophyte may be developed on a gametophyte. The structure bears a striking resemblance to a seed of certain seed-bearing plants, and, for that reason, Selaginella has become a fruitful field for speculation with reference to the origin of the seed habit. We are content here to call attention to certain points of resemblance between the condition shown in Fig. 389, A and a seed, and at the same time to indicate what Selaginella lacks in producing a real seed as found in the Spermatophyta.

Since the tissue of the megagametophyte is homologous with the endosperm in certain seeds, as in Gymnosperms, the embryo sporophyte of Selaginella, with its surrounding gametophyte tissue, is comparable to the embryo and surrounding endosperm of a seed. However, Selaginella falls short of developing a seed in the following respects: there is nothing homologous with a definite seed coat, and the embryo does not pass into a dormant state as in the seed of seed-bearing plants. In all Pteridophytes the development of the embryo from the zygote is a continuous and uninterrupted process until the embryo has established itself in the soil.

The foregoing statements are not intended to convey the idea that Selaginella represents the ancestral condition of the seed plants. Their purpose is merely to show what progress Selaginella has made toward the seed habit. There are reasons to believe that seed plants took their origin among certain heterosporous Pteridophyta. Heterospory is a condition found in all seed plants, and their ancestors were undoubtedly heterosporous. With reference to the embryo and its surrounding gametophyte, certain seed characters may be recognized in the Ophioglossaceae.

Isoetaceae.—This family is represented by the genus Isoetes, species of which occur in our flora. The plants are commonly known as Quillworts. They bear no external resemblance to other Pteridophyta. The sporophyte resembles a tuft of grass or small rushes (Fig. 390, A). It consists of a very short, flattened stem bearing numerous roots and onion-like leaves. Each leaf has a broad base, just above which is the ligule (Fig. 390, B). The leaf bases overlap and conceal the stem. Isoetes is heterosporous. The sporangia are borne at the base of the leaves on the adaxial side. The outer leaves of each cycle bear microspores, and the inner, megaspores. The innermost leaves, which are sterile and not fully developed, separate one year's growth from the next. The oval sporan-

gium is sunk in a depression whose margin, the *velum*, may almost completely cover the sporangium. The gametophytes are similar in character

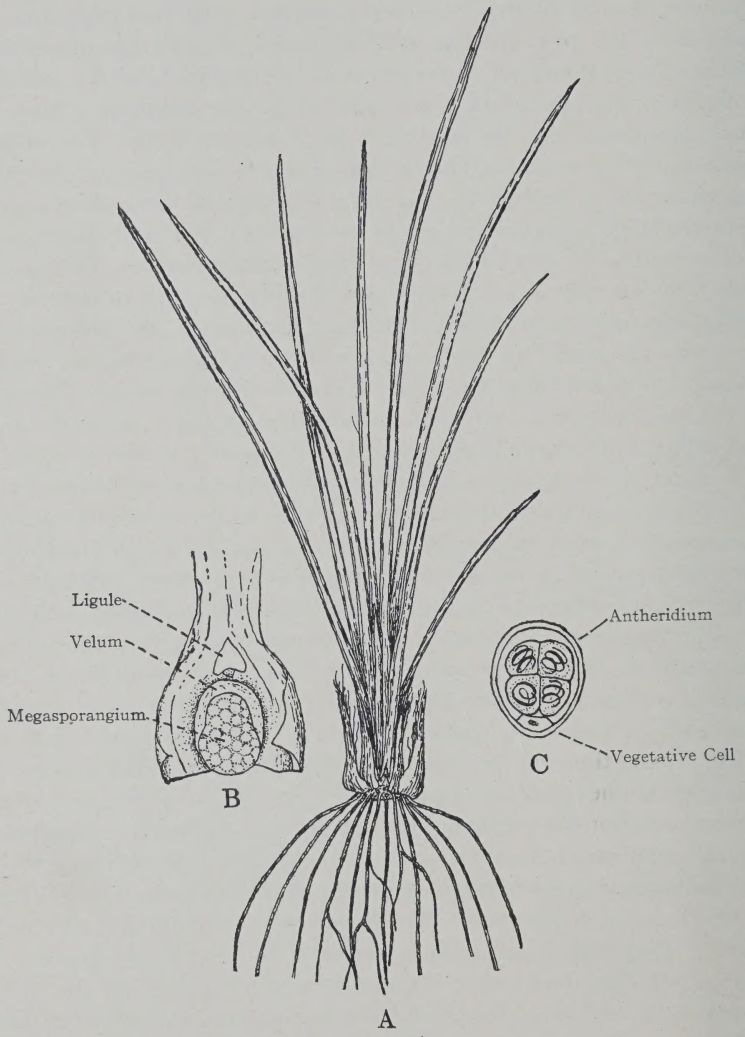


FIG. 390.—Isoetes. A, habit of sporophyte. B, base of leaf with megasporangium. C, microgametophyte, consisting of one vegetative cell and one antheridium with four sperms. (C, from Campbell's "Mosses and Ferns." By permission of the Macmillan Company, Publishers.)

to those of Selaginella. The structure and development of the whole plant suggests in many ways a monocotyledonous seed plant. The micro-

gametophyte is reduced to a single prothallial cell and an antheridium bearing four biciliate sperms (Fig. 390, C).

Fossil Pteridophyta.—In the period of geologic time known as the Paleozoic age, the majority of Ferns, as revealed by known fossils, were plants resembling the living Marattiaceae. Many of the Horse-tails and Club-mosses attained the size of lofty trees, constituting the forests of the humid regions of the earth. Those that exist today may be looked upon as the degenerate remnants of the gigantic forms once prevailing in great numbers,—the mere ruins of a magnificient flora. The Pteridophyta of that time contributed largely to the formation of the coal deposits of the earth.

Plants Which Were Made into Coal.—Many persons have learned from one source or another that the coal we burn in stove and furnace is of vegetable origin, but few are aware of the kinds of plants involved. It is also well known that coal is now found beneath layers of rock of many feet in thickness. Two questions arise: what plants contributed to the formation of coal? and how did the coal come to be covered with rock?

Upon those parts of the earth's surface in which coal is found there grew millions of years ago—how many millions no one knows—numerous ferns, horsetails and club mosses. Many of the horsetails and club mosses were of gigantic size, being as large as our beech and maple trees. The localities in which this vegetation grew were low and marshy, somewhat like our peat bogs of today. The climate was humid and supposedly warmer throughout the year than at present. One of these localities was a part of southwestern Indiana and the adjacent portion of Illinois in which coal is found. The marshy regions were low valleys, surrounded on two or more sides by hills or mountains. The valleys and highlands were formed during those ages by great wave-like foldings or wrinklings of the earth's crust, the valleys occupying the low places.

The conditions which favored the growth of vegetation in the marshy valleys continued for many ages. The stems, roots, and leaves fell where they grew, but they did not decay, or only in part. The character of the water and soil did not favor the growth of organisms of decay, and the remains of vegetation accumulated year after year.

The wrinkling and folding of the earth's crust continued so that the valleys sank lower and the upheavals became higher, for the great mountain ranges were not completely formed. The slow sinking of the valleys permitted the accumulation of a greater depth of vegetable remains. Finally these marshes with their accumulation of plant material sank so low that the sea flowed in covering all. The vegetable remains then lay at the bottom of the sea. During ages which followed there were deposited at the bottom of the seas upon the accumulated remains of forests of horse-

tails, club-mosses and ferns, layer upon layer of rock, totalling many feet in thickness. Because of the great weight, the growth of microorganisms, and as a result of oxidation, the vegetable remains were changed into the black material which we know as coal.

With the subsequent upheavals during the final shaping of the earth's crust the ancient valleys with their deposits of coal and overlying rock were again elevated above the level of the sea forming the land surfaces of the present time.

In certain deposits of coal beautiful imprints of leaves, stems, and fruits are found. Some of these are so perfect that the skilled geologist is able to know definitely the families and species to which the plants belonged.

While much of the coal was due to ferns and fern-like plants, as stated above, that which was formed in later ages contain the remains of such trees as pines, cedars, etc.

It may be mentioned that our oil and gas obtained from rock beneath the surface were of organic origin, both animal and vegetable life contributing.

Comparison of Fern and Moss.—A comparison of the life of the fern with that of the moss will show some very striking contrasts, especially in regard to the sporophyte:

Gametophyte

Moss	Fern
1. Large, leafy axes; with tissues somewhat differentiated.	1. Very small, flat and heart-shaped thallus with a simple structure.
2. May live from year to year, or indefinitely, producing sporophytes each year.	2. Lives a short time; produces but one sporophyte.
3. Not exhausted by the sporophyte.	3. Completely exhausted by the sporophyte.

Sporophyte

1. A slender stalk and capsule. Tissues slightly differentiated.	1. Differentiated into root, stem, and leaf, with highly differentiated tissues including a vascular system.
2. Dependent upon gametophyte.	2. Becomes independent of gametophyte.
3. Lives but one season.	3. Lives from year to year or indefinitely.

The Role of the Pteridophyta in the Evolution of Plants.—Viewing the Pteridophyta and Bryophyta from the standpoint of evolution, i.e., from that of progressive development, we find that the greater advance has been made by the sporophyte, or diploid structure. The large independent sporophyte of the seed-bearing plants, with roots, stems, leaves and vascular tissues, has already been attained by the Pteridophyta. The

sporophyte has added those parts which were not present in that of the moss. Evolution has been progressive.

In regard to the gametophyte, however, that structure is simpler than the moss gametophyte. It probably has undergone a loss; its evolution has been regressive and not progressive.

Pteridophyta living at present do not bear seeds, but they have made progress toward the production of seeds. All seed plants bear two kinds of spores, large and small. The higher Pteridophyta bear the two kinds of spores, and a structure approaching a seed. This structure is seen in Selaginella at the stage of development shown in Fig. 389. Here the embryo surrounded by the tissue of the gametophyte is comparable to a seed with embryo and endosperm. The embryo of Selaginella does not pass into a dormant state, and a cover for the whole, like that of a seed coat, is lacking. Selaginella almost developed a seed.

These and other facts presented in the life histories of liverworts, mosses, and ferns, supply undeniable evidence in behalf of the doctrine of descent, namely, that existing organisms were derived from preexisting forms, and that all living things are related.

Evolution means the progressive and orderly development in nature. When we say that Bryophyta and Pteridophyta are related we mean that their ancestral forms were closely related. We do not mean that ferns were evolved from any liverwort which now exists. No liverwort now existing can ever become a fern. Every species of liverwort can only become more liverwort-like, and all mosses can only become more moss-like.

Furthermore when we say that such Pteridophyta as Selaginella and the Quillwort, Isoetes, came near developing a seed, we mean that they point to the probable way by which a seed was brought about in nature. We do not mean that Selaginella or Isoetes will ever give rise to seed plants.

TOPICS FOR REVIEW AND DISCUSSION

What are the diploid and haploid structures in the life history of a fern.

How does the sporophyte of the fern differ from that of the moss?

What does the word *frond* mean as applied to the fern?

What are the following: A pinna? A pinnule? A sorus? An indusium? A false indusium?

What is the annulus?

Explain how the annulus opens the sporangium.

Do you know of a fern in which the sporangium does not have an annulus?

How is the young leaf of a fern folded in the bud?

Does the fern leaf continue growth at the tip or near the base?

If one injures the tip of a fern leaf, will it continue to grow at that point?

How are wounds healed at the point of injury?

Do you know any native ferns whose leaves remain green all winter?

What does the expression "Christmas fern" mean?

Do you know of a fern in which the stem (rhizome) produces runners? Does the runner end in a bud?

How do florists propagate the so-called Boston fern (Nephrolepis)?

What is the "walking fern"? Why is it so named?

Give four ways in which the fern sporophyte may propagate vegetatively.

Do fern roots ever spring from near the bases of the leaves?

Do you know of a native fern whose roots develop adventitious buds?

Compare the gametophyte of the fern with that of the liverwort, bringing out the important differences.

By what other name is the gametophyte known?

In the evolution from liverwort to fern does the gametophyte become more complex or less complex?

The gametophyte of what liverwort, do you think, bears the closest resemblance to the fern gametophyte?

What four regions are readily recognized in the early development of the embryo? Which two develop more rapidly?

What is heterospory?

Name three heterosporous Filices.

What gametophyte develops from the microspore? From the megaspore?

How large are those gametophytes in comparison with the size of the respective spores?

Do those gametophytes develop chlorophyll to any extent? From what source do they secure their food?

What are the horse tails, or scouring rushes?

In what respects does the sporophyte of Equisetum differ from that of the fern?

What family of the Lycopodinae is heterosporous? Which is homosporous?

Where do the gametophytes of Lycopodium usually grow?

The gametophyte of what fern develops in the soil?

What is apogamy?

What is apospory?

At what step in the life cycle of the fern does the reducing nuclear division take place?

Write a diagram of the life cycle of the fern beginning with the adult sporophyte.

Write a diagram of the life cycle of Selaginella beginning with the sporophyte. (It should be borne in mind that life cycle diagrams may be expressed in different ways, and that each student should be able to write his own diagrams, using those in the text merely as suggestions. Diagrams may be brief or detailed.)

What progress have the Pteridophyta made toward the evolution of the seed plants?

What Pteridophytes do you think have made the greatest progress toward the seed habit?

What Pteridophytes in past ages were as large as forest trees?

What Pteridophytes have contributed to the formation of coal?

Coal was made from peat or vegetation which grew upon the surface of the earth. How came the coal to be deeply buried beneath rock?

Can you imagine how the sporophyte of Anthoceros might so change as to give it the rank of a fern?

What plants do you think the remote ancestors of the ferns resembled?

What is progressive evolution?

What is regressive evolution?

Cite instances from the Bryophyta and from the Pteridophyta.

Are the terms, gametophyte, prothallium and haploid structure, synonymous?

What are bisexual, or monoecious prothallia? Where upon the prothallium are the archegonia borne?

Where are the antheridia borne upon a monoecious prothallium?

Are prothallia which are one cell in thickness able to bear archegonia?

May fern gametophytes propagate vegetatively? Under what conditions?

Who was Eduard Strasburger? To what phase of modern botany was he a voluminous contributor?

To the knowledge of what group of plants has Douglas H. Campbell been a large contributor?

CHAPTER XVIII

SPERMATOPHYTA—GYMNOSPERMS

The Spermatophyta include all those plants which bear seeds as well as microspores and megaspores. There are two great groups, Gymnosperms and Angiosperms. In the Gymnosperms the seeds are borne on open megasporophylls, (*carpels*), as in the pine cone, while in Angiosperms the seeds are developed within closed carpels (*pistils*). In the common pea, for example, the pod is the closed carpel.

GYMNOSPERMS

The Gymnosperms, which are commonly known as our evergreens, such as pines and cedars, are subdivided into four orders: (1) the cycads (Cycadales), (2) the Ginkgo tree (Ginkgoales), (3) the conifers (Coniferales), and (4) the gnetums (Gnetales). Of these the conifers are the most important and most widely distributed upon the Earth at the present time. Those which are more commonly seen in woods, parks, and private grounds are the pines (Pinus); the spruces (Picea); the firs (Abies); the hemlock (Tsuga); the red cedar, or juniper (Juniperus); the arbor-vitae or white cedar (Thuja); the white cedars or cypresses (Chamaecyparis); the bald cypress of our southern states (Taxodium); the larches, or tamaracks (Larix); the yew trees (Taxus); and the Douglas fir, or Oregon pine (Pseudotsuga). Here belong also the redwoods (Sequoia) of the Pacific coast states. The larches, bald cypress, and the Ginkgo tree are deciduous. The others are evergreens.

The Ginkgo tree, a native of Asia, is widely cultivated, being quite hardy in our climate. It is of special interest from the botanical standpoint, because of the fact that its ancestry can be traced farther back in the history of vegetation than any other living species. Its leaves resemble those of the maidenhair fern.

The cycads are mostly tropical and sub-tropical. While they resemble palm trees in form, they are more closely related to the ferns. Their leaves, like those of ferns, are coiled up in the bud like a watch spring, and the sperms are motile.

The gnetums (Ephedra, Gnetum) are chiefly tropical and subtropical. Some have broad leaves and behave in growth like the great lianas. Those of our arid southwest are switch-like plants with jointed stems and greatly reduced scale-like leaves.

As a sample of the life history of a gymnosperm, a species of pine has been selected for discussion in the following paragraphs.

The Pine Tree, the Sporophyte

The following description of the life history of a gymnosperm will pertain to a common pine, such as the Austrian, or black pine (*Pinus*

Fig. 391.—Young tree (sporophyte) of white pine, *Pinus strobus*. Note the tendency of the long branches to arise in whorls on the main stem or trunk.

nigra), the Scotch pine (*Pinus sylvestris*), or the white pine (*Pinus strobus*).

The typical pine tree has a main stem, or trunk, extending from the ground straight up to the tip which ends in a terminal bud (Fig. 391). The terminal bud extends the growth of the trunk, and from near its base arises a circle of lateral buds. The trunk is continued straight down-

wards into the earth as a tap root, from which spring numerous, branching, secondary roots.

From the trunk grow out at regular intervals more or less horizontally long branches that tend to be arranged in circles. The branches springing from the trunk develop other branches, varying in length, which tend to spread out in the intervening spaces. All of these long branches are of unlimited growth and each ends in a terminal bud.

All of the long branches and the youngest part of the trunk bear numerous, very short dwarf shoots of limited growth. The dwarf shoots of the white pine end each in five needle-shaped foliage leaves, those of the Scotch and Austrian pines bear two needles each, and those of the

FIG. 392.—A, a mature and opened ovulate cone of black or Austrian pine, *Pinus nigra* (*Pinus austriaca*). B, a seed, natural size.

pitch pine (*Pinus rigida*) three needles. Both dwarf and long branches bear scale leaves.

The foliage leaves of the black pine, for example, live three or four years as a rule; consequently, after the tree is three or four years old, some leaves are shed annually. In some species the leaves remain on the tree many years.

The Pine Cone, or Strobilus.—The fruit of the pine tree is the seed-bearing cone (Fig. 392, A). This cone consists of a number of hard, horny scales, *carpels*, closely and spirally arranged upon an axis. About one-half or more of the carpels, those at the basal end, bear no seeds. Each carpel of the upper portion of the cone bears one or two seeds at its base on the adaxial side (Fig. 398, C, *c*). After the cone is mature

and dried out the carpels spring apart liberating the seeds which separate from the carpels.

The Seed.—The seed of the pines here under consideration is provided with a thin membranous wing (Fig. 392, B). The wing is split off from the surface of the carpel. The seed consists of a centrally placed embryo surrounded by the endosperm. The seed coat is separable into two visible layers, an outer, thick, hard part and a very thin, brown, papery membrane. The micropyle is at the more pointed end (Fig. 393, A).

The cylindrical embryo has a number of cotyledons (Fig. 393, B). From the lower end of the hypocotyl the primary root will develop. At the lower end of the embryo is a delicate coiled thread, the *suspensor*.

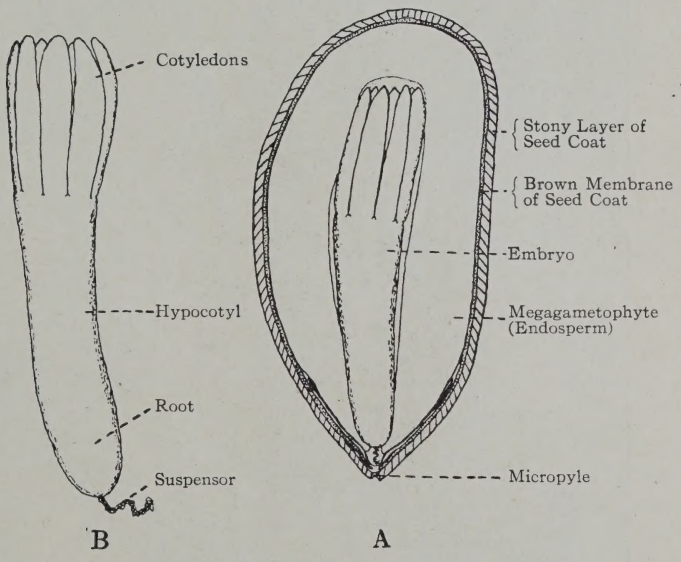


FIG. 393.—*Pinus edulis*. A, longitudinal section of seed with embryo in position. B, embryo removed from the seed, enlarged.

The Development of the Seed in Pinus.—As already stated, seed-bearing plants produce spores also. Before seeds and fruit can be formed flowers must be developed, for gymnosperms bear flowers as well as do angiosperms. What constitutes a flower depends, of course, upon our definition of the term. Here a flower means one or more spore-bearing parts (sporophylls) of either stamens (*microsporophylls*) or carpels (*megasporophylls*) borne upon an axis.

In the pine there are two kinds of flowers which bear the two kinds of spores. The staminate flowers bear microspores (pollen) and the ovulate

flowers bear megaspores. Both kinds of flowers are in the form of cones (strobili).

The Staminate Cone.—The staminate cone consists of many stamens (*microsporophylls*) closely arranged upon the axis. These cones are borne near the base of the shoot of the season's growth (Fig. 394, right and Fig. 395). Each stamen, which is triangular in outline, bears two *micro-*

FIG. 394.—Young shoots of *Pinus densiflora* bearing flowers; staminate cones at the right, ovulate at the left.

sporangia (pollen sacs) on the abaxial side (Fig. 396, A). In Fig. 396, B, are shown four stamens attached to the axis of the cone. The two at the left are seen from the surface in profile, the two at the right in longitudinal section. A cross section of a stamen is shown in Fig. 396, C. From this is seen the relation of the two sporangia to the rest of the sporophyll.

When mature each sporangium opens by a longitudinal slit and liberates the *microspores* which are commonly known as *pollen spores*, or pollen grains. After the pollen is shed the staminate cone dries up and soon falls from the tree.

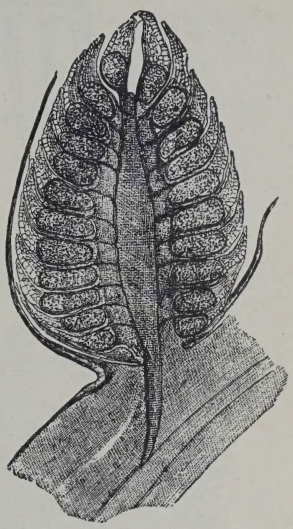


FIG. 395.—Longitudinal section of a staminate cone of *Pinus montana*. (Strasburger, Macmillan Co.)

The Microspore.—In the developing microsporangium, the pollen spores are formed from a mass of large cells termed microspore mother-cells. Each mother-cell gives rise to four spores. As in the Pteridophyta and Bryophyta, the four spores derived from a spore mother-cell constitute a spore tetrad (Fig. 397, A). The first nuclear division in the spore mother-cell is a reducing division, consequently, each microspore possesses the single number of chromosomes. Immediately following the tetrad divisions and the dissolution of the wall of the spore mother-cell, each spore develops a firm cell wall of two layers, the outer layer being the exine, and the inner the intine. At two places on opposite sides of the spore, the exine separates from the intine, and air enters the opening. There are thus formed two inflated appendages, the "wings" of the spore (Fig. 397, B). Before the sporangia are mature, each spore produces, by three successive divisions, a series of three small cells within, called prothallial cells. Two of these cells disorganize soon after they are formed, leaving the third, which will be known as the antheridial cell. The pollen spore at the time of the opening of the sporangium consists, therefore, of the large tube cell, and, within, at the dorsal side of the spore, the antheridial cell and the remains of two disorganized prothallial cells (Fig. 397, B).

The pollen, as it falls from the sporangia, is light, dry and readily blown about by the wind.

The Ovulate Cone.—The ovulate strobilus consists of a number of carpels (*megasporophylls*) closely and spirally arranged on the axis (Fig. 398, A). Each carpel is triangular in outline and attached to the axis by a very short stalk. It bears two ovules (*megasporangia*) (Fig. 398, A, *a*). At the lower end of each ovule is a small cleft, the *micropyle*, in which the pollen must be deposited in order to function. The complete megasporophyll consists of a small bract, from whose adaxial side, near the base, is developed the large ovuliferous scale, which later becomes the bony carpel. By the time the flower is in bloom the ovuliferous scale

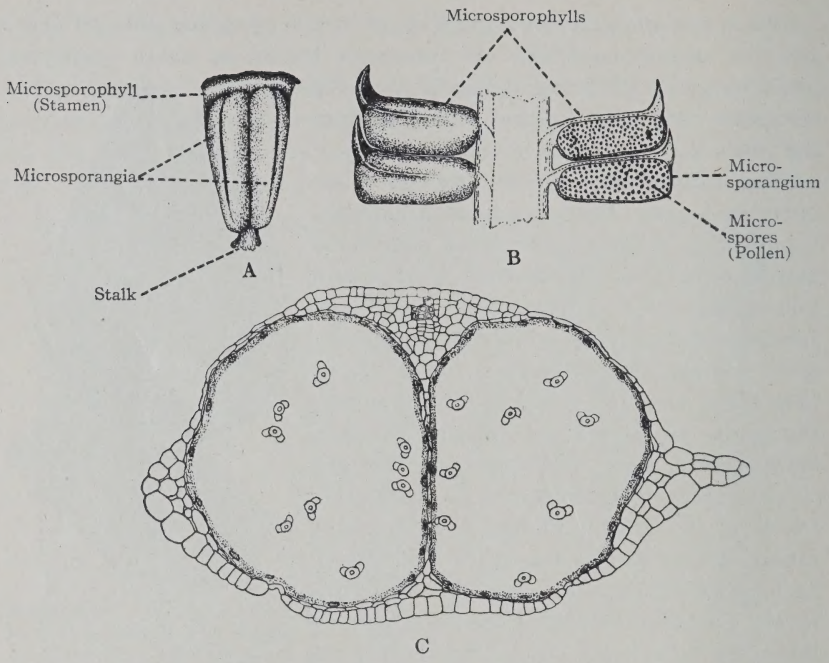


FIG. 396.—Parts of a staminate cone of *Pinus nigra*. A, abaxial view of a stamen, microsporophyll, showing the two microsporangia opening by longitudinal dehiscence. B, portion of the axis of the cone with two stamens at the left in surface view and two at the right in longitudinal section. C, cross section of stamen magnified.

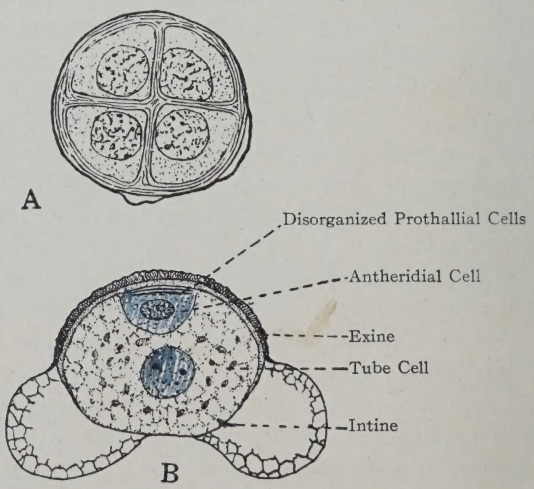


FIG. 397.—Pollen spores, microspores, of *Pinus nigra*. A, pollen mother-cell containing a tetrad of pollen spores. B, mature pollen spore.

is larger than the bract, which is seen in the abaxial view (Fig. 399, B). The relation of bract, ovuliferous scale, and ovule is readily seen in a

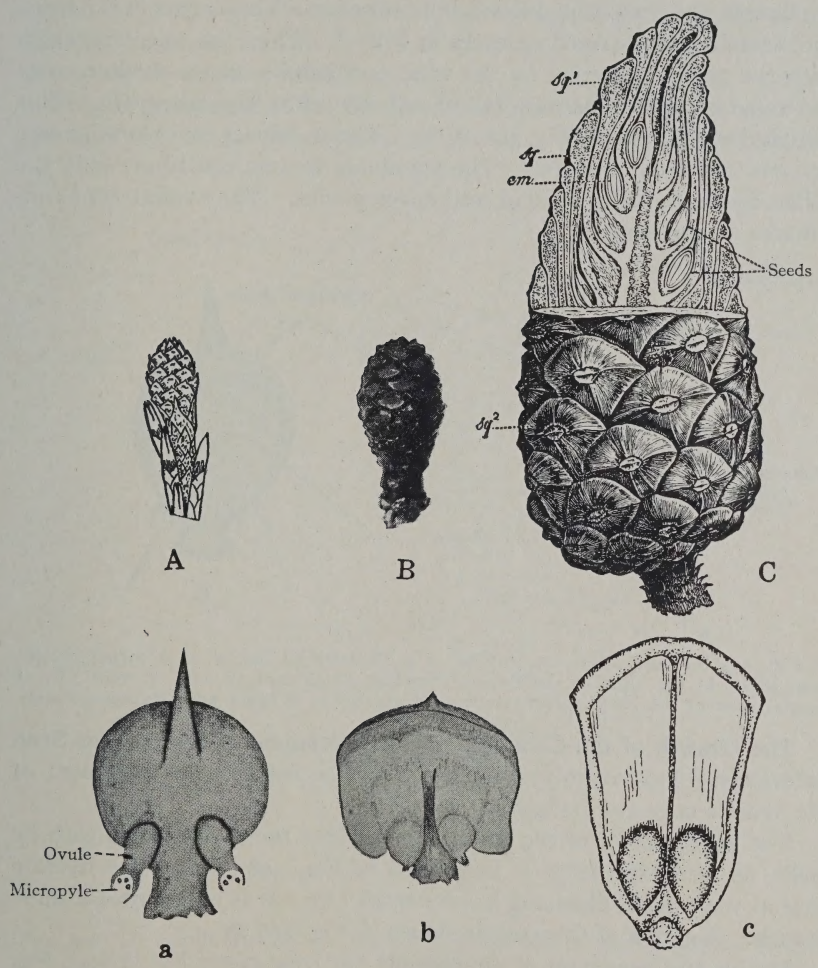


FIG. 398.—Stages in the development of the pine fruit and seed as seen externally. A, ovulate cone (*Pinus nigra*) at the time of flowering somewhat enlarged; *a*, one carpel enlarged as seen from the upper, or adaxial side. B, ovulate cone one year old, natural size; *b*, one carpel of the same enlarged. Note the wings of the future seeds are outlined. C, mature ovulate cone (*P. sylvestris*) with an upper one-fourth cut away; *c*, one carpel with the two seeds in position; *sq*, carpels; *em*, embryo. (C, from Bessey.)

longitudinal section, as shown in Fig. 399, A. In the Austrian pine both staminate and carpellate flowers are borne on the same tree. When this is true the tree (sporophyte) is monoecious. If, as in some gymnosperms,

the red cedar for example, the staminate flowers are borne on one tree and the ovulate flowers on another, the sporophyte is dioecious.

Pollination.—The pine tree blooms when the winter buds containing the flowers open, exposing the strobili to the air. This occurs in the black and Scotch pine in April or early in May.* When the microsporangia open the pollen is carried by the wind and gravity to the ovulate cone, and some of the spores may fall or roll down into the micropyle. This constitutes pollination (Fig. 398, A, *a*). The staminate cones now become dry and fall from the tree. The staminate flowers contribute only the pollen spores to the process of seed development. The ovulate cone contributes all the rest.

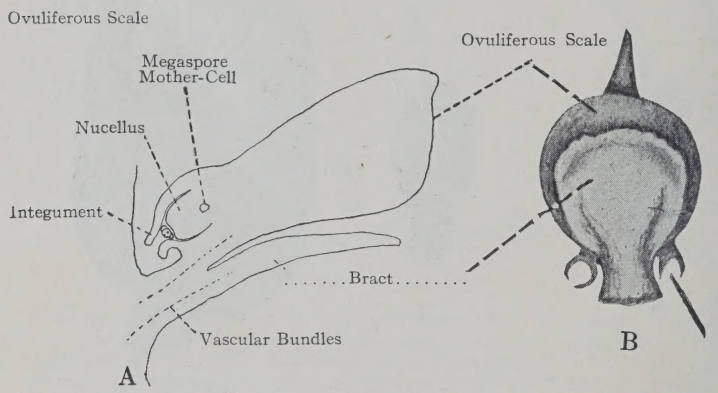


FIG. 399.—*Pinus nigra.* A, outline of a longitudinal section of a carpel (Megasporophyll) at the time of pollination showing attachment to axis of cone. B, an abaxial view of the same carpel, showing relative size of bract and ovuliferous scale.

The Growth of the Cone and the Development of the Seed as Seen Externally.—Two years are necessary for the complete development of the ovulate cone and its seeds.

The development of the ovulate flower into the mature cone with its seeds, as seen externally, is illustrated in Fig. 398, A-C. The ovulate cone at the time of blooming is very small (A). It is borne upon a short branch. A carpel of this cone is shown in Fig. 398, A, *a*.

During the remainder of the summer the cone grows but little. Fig. 398, B is an ovulate cone of *Pinus nigra*, natural size, at the close of the first summer. Below it (B, *b*) is a carpel of the same enlarged. The micropyles are closed, and the wings of the future seeds are outlined upon the surface of the carpel. In this condition the cone passes the winter.

In the following April, just about one year after pollination, the year-old cone begins a rapid growth, attaining the adult size about June 1st (Fig. 398, C). It is green in color and soft enough to be cut easily with

*The dates given in this chapter refer to the Ohio valley.

knife or scalpel. One carpel with the two ovules which have attained the size of the mature seeds are shown at C, *c*. These young seeds are not mature internally, i.e. embryos are not present in them. During the remainder of the growing season of the second year, the ovules mature internally into the mature seeds, and the carpels become hard and brown fitting tightly against each other (C).

The Development of the Seed as Seen Internally.—We may now turn our attention to the development which takes place inside the ovules as

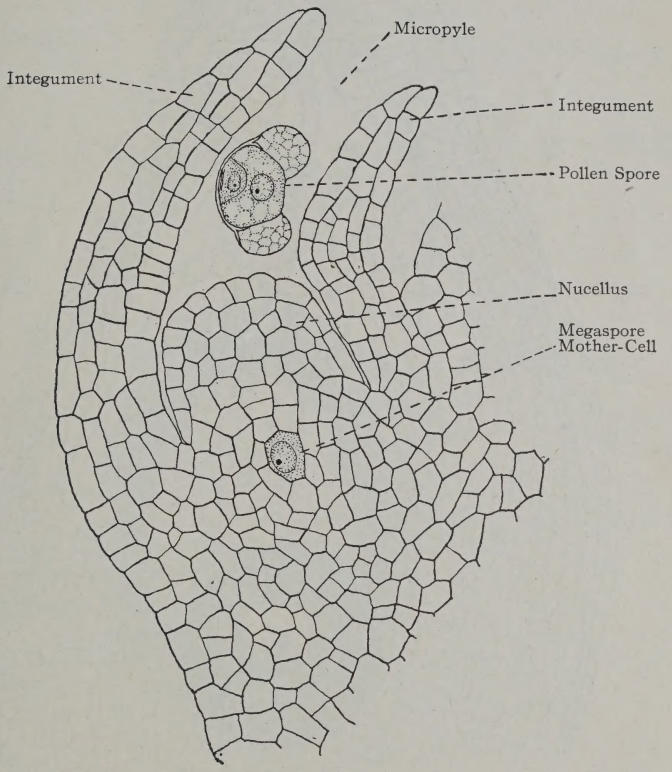


FIG. 400.—Longitudinal section of the ovule of Fig. 398, *a*, showing internal structure in detail.

shown in Fig. 398, A-C. A median longitudinal section of an ovule at the time of pollination will reveal the interior of the ovule of Fig. 398, A, *a*. Such a section is shown in Fig. 400. It will be seen that the ovule consists of a central mass of cells, the *nucellus*, surrounded by a layer of tissue four or more cells thick, the integument. The integument grows up beyond the free end of the nucellus, but does not close completely. The small opening remaining is the *micropyle*, in which one or more pollen spores may be found. Deeply situated in the nucellus is the well defined

megaspore mother-cell. From this cell a tetrad of four potential megaspores is formed, but only one, as a rule, is functional, the other three being consumed as food by the functional megaspore, which gives rise to the *megagametophyte* (*endosperm*).

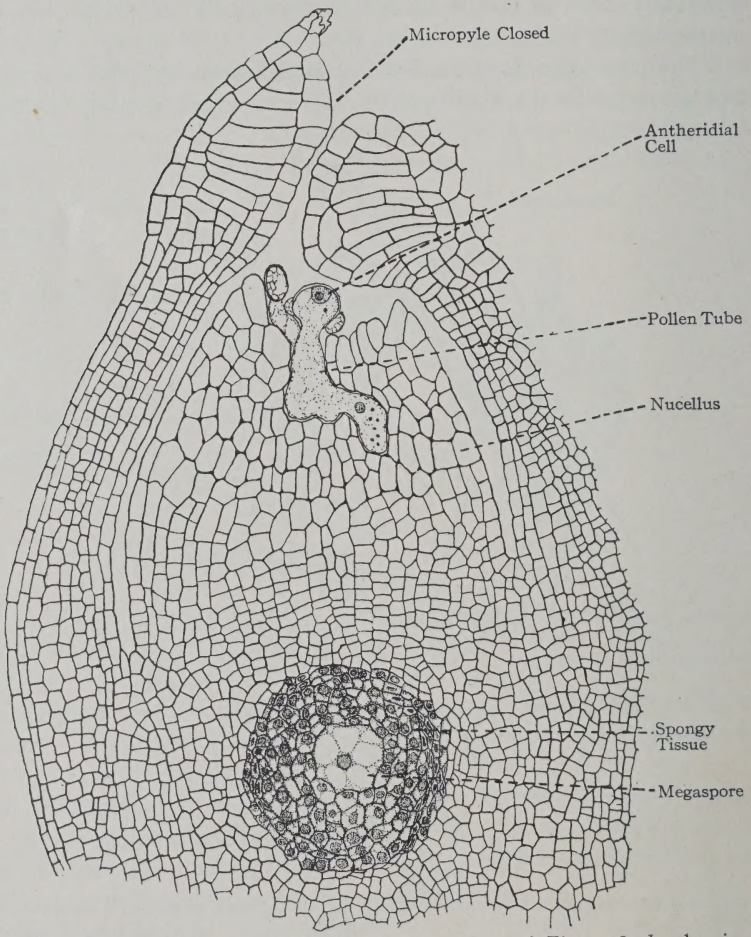


FIG. 401.—Longitudinal section of the one-year-old ovule of Fig. 398, *b*, showing internal structure.

The first nuclear division in the megaspore mother-cell is a reducing division, hence the nucleus of the megaspore contains the single number of chromosomes. The nuclei of the megagametophyte contain, therefore, the single number of chromosomes.

The Ovule at the End of the First Season's Growth.—Two years are necessary for the complete development of the pine seed. During the

first summer following pollination the ovulate cone increases in size from that of Fig. 398, A, left, to that of Fig. 398,B. It is evident that little growth occurs during the first summer. During the first season the micro-

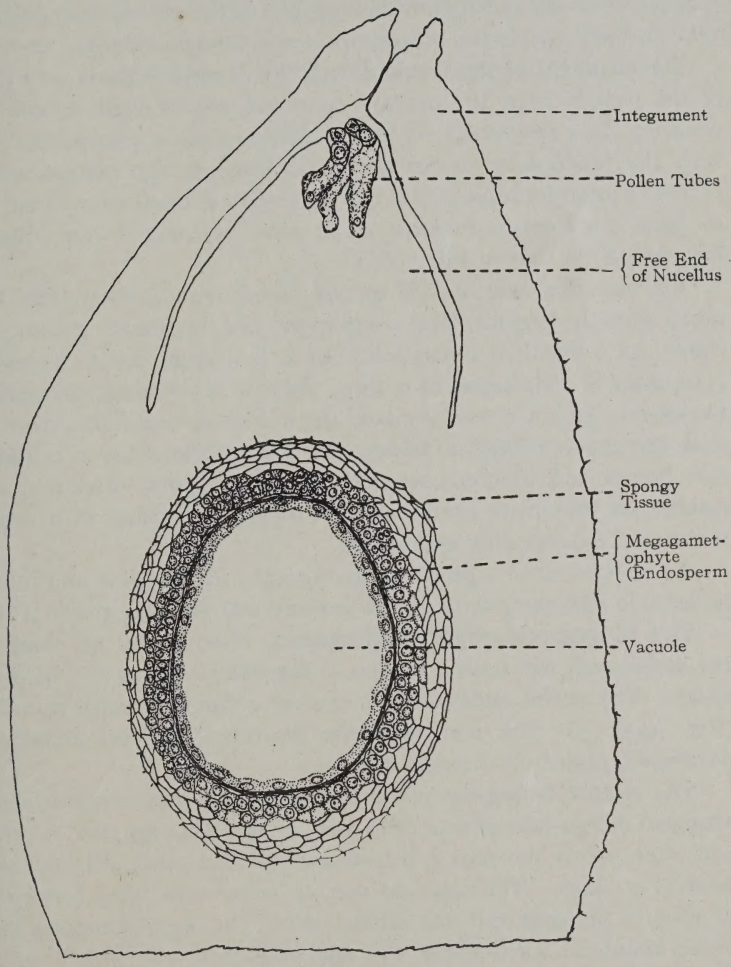


FIG. 402.—Longitudinal section of an ovule shortly after the beginning of rapid growth in the second year.

spores and megaspores begin their development into gametophytes. A median longitudinal section of an ovule at or near the close of the first year's growth is shown in Fig. 401. The micropyle is now closed. The tube cell of the germinating pollen spore has formed a short tube, which takes

a downward* course in the nucellus. The antheridial cell is unchanged. The megaspore has greatly enlarged at the expense of the nutritive tissue immediately surrounding it, the *spongy tissue*, which is specially developed from the nucellus. In the megaspore a number of nuclei may be present. The pollen spore and its developing tube is the *microgametophyte*, and all that develops inside the megaspore is the *megagametophyte*, or *endosperm*.

Development of the Ovule during the Second Season.—In the spring of the second year, the ovulate cone and ovules begin a rapid growth, resulting, in a few weeks, in a cone seven or eight centimeters in length with the functioning ovules almost as large as the mature seed. The period of rapid increase in size in *Pinus nigra* extends from about April 20 to June 1 in central Indiana. The cone increases in size from that of Fig. 398, A, to that of Fig. 398, C.

Fig. 402 is a longitudinal section of an ovule a short time after the rapid growth begins. The megaspore has increased greatly in size, chiefly as a result of hydration. In it is a large central vacuole. The cytoplasm is distributed in a thin, uniform layer along the periphery of the spore. In it are evenly spaced the numerous nuclei that have resulted from successive nuclear divisions. In this peripheral layer, cell formation now begins and proceeds regularly in a centripetal direction, with the result that the entire cavity of the megaspore is filled with the cellular tissue of the developing endosperm.

As referred to in a preceding paragraph, the nucellus and integument increase in size along with the megaspore and all other parts of the cone.

The Megagametophyte (Endosperm).—About the last week in May the endosperm will have completely filled the large cavity of the megaspore. The entire endosperm is oval or cylindrical, with rounded ends (Fig. 403). At the end near the micropyle several archegonia are developed, each from a single cell.

The mature archegonium consists of a small neck of about eight cells, arranged in two tiers of four cells each, a very large egg, and a very small, and often poorly developed, lens-shaped ventral canal cell just below the neck (Fig. 404). The egg and ventral canal cells were formed by the division of the large cell, the central cell. The layer of regular cells with dense contents, surrounding the egg, constitute the jacket, or mantle. These cells contribute nourishment to the egg, their function being of the nature of a tapetum.

As the archegonia develop, the endosperm tissue grows up beyond them, and consequently a narrow passage, or canal, leads down to each archegonium (Fig. 404).

* In these pages *up* means in the direction of the micropyle, while *down* is the opposite direction, or toward the base of the nucellus.

When the pine archegonium is compared with that of the ordinary fern, it is seen that this organ in the pine has a greatly reduced neck, which doubtless has no function. The neck canal cell is absent, and the ventral canal cell is evanescent, or it may not be completely organized. The archegonium of the pine, in the poorly developed neck, the loss of a neck

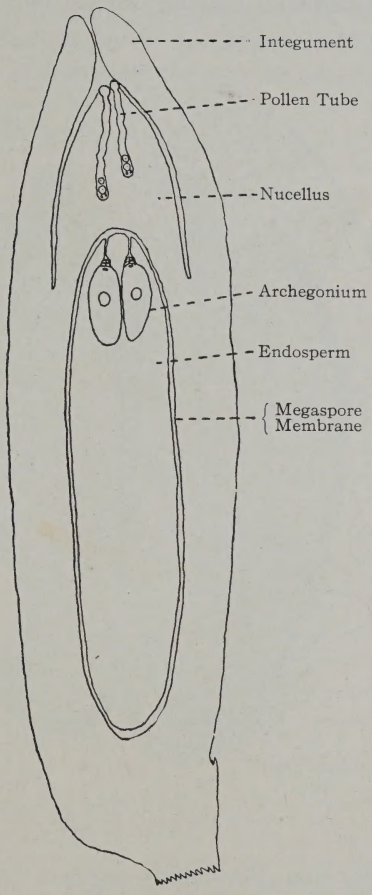


FIG. 403.—*Pinus nigra.* Outline drawing of a longitudinal section of an ovule a short time before fecundation.

canal cell, and the reduced ventral canal cell, represents one of the best illustrations of regressive evolution among reproductive organs in the plant kingdom. Evolution through loss of parts (failure to develop) is further illustrated in one of the highest gymnosperms, to be mentioned later, namely, Gnetum, in which no archegonium is formed. The surviving remnant is an egg nucleus, or perhaps a poorly differentiated cell.

The Microgametophyte, or Pollen Tube.—Let us recall again that all which develops inside the megaspore is megagametophyte, or endosperm, and that this endosperm bears a number of archegonia at its upper end. For the same reason all that develops from the microspore, or pollen grain, is the microgametophyte, or pollen tube, in which is developed a rudimentary antheridium bearing two *sperms* (Fig. 405). *Both gameto-*

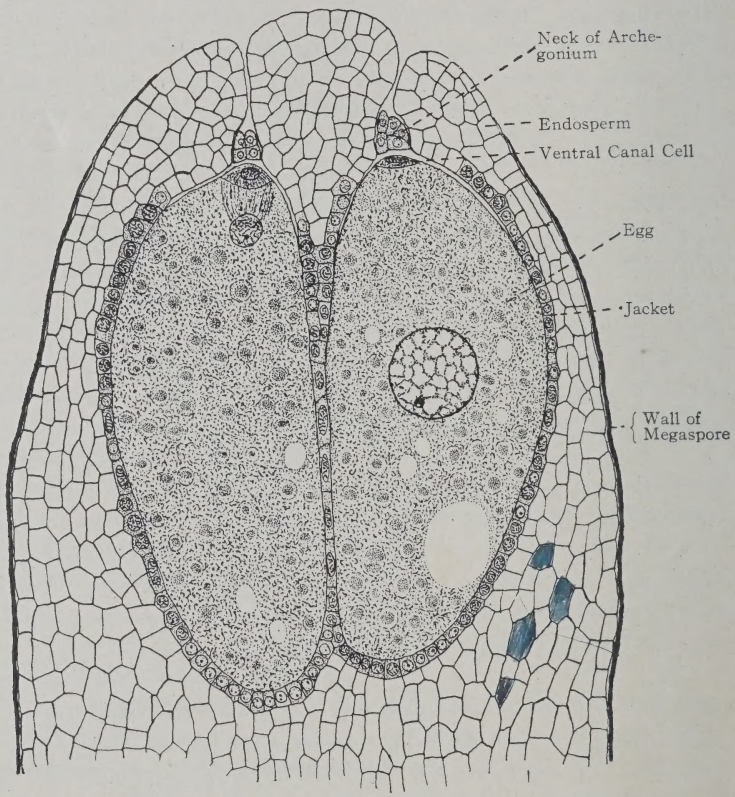


FIG. 404.—*Pinus nigra*. Longitudinal section of the upper end of the endosperm, showing two archegonia. The one at the right is mature and ready for fecundation; that at the left is younger; the ventral canal cell is being cut off.

phytes grow parasitically within the tissue of the nucellus. They are the haploid individuals.

During the growth of the pollen tube through the nucellus in the second season, the following development takes place within it: the antheridial cell divides into a stalk cell and a body cell (Fig. 405, A); the body cell enlarges, and both move from the cavity of the spore down into the growing end of the tube; the stalk cell remains the same or tends to disintegrate;

the nucleus of the body cell divides to form two sperm nuclei. The body cell itself does not divide in *Pinus nigra* (Fig. 405, B). Since it is not surrounded by a cell wall, but by a plasma membrane only, the outline of the body cell is not always clearly discernible. The mature microgametophyte consists, therefore, of the pollen tube, in which are the two sperm nuclei, the tube nucleus, and the remains of the stalk cell.

Fecundation and Development of the Embryo.—The distal end of the pollen tube continues growth down through the nucellus and the upper

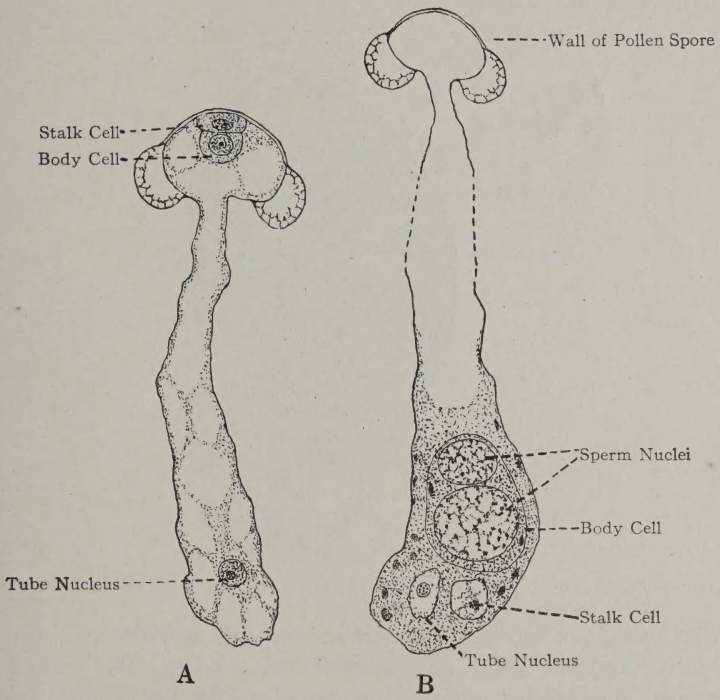


FIG. 405.—*Pinus nigra*. Two microgametophytes, pollen tubes, in different stages of development. A, the antheridial cell has divided into the stalk cell and the body cell. B, the proximal and distal ends are shown. The proximal end is empty. In the distal end are the large body cell with the two sperm nuclei, the stalk cell and the tube nucleus.

part of the endosperm until it reaches the egg. When in contact with the egg an opening is dissolved in the end of the tube through the action of an enzyme, and the contents are discharged into the cytoplasm. One sperm nucleus, the larger, which is usually nearer the end of the tube, functions, while all the rest of the contents is digested as food. The functional sperm nucleus passes to the nucleus of the egg, and both unite as the first nuclear division of the zygote takes place (Fig. 406).*

* The details of this process are too complicated to be given here.

Following the first nuclear division in the zygote, the two resulting daughter nuclei divide in a very short time. The four free nuclei pass to the bottom of the zygote (the end farther from the micropyle) and lie in a horizontal plane (Fig. 407). Two of the four nuclei are shown in the zygote at the right. These four nuclei divide, and cell division follows, so that two tiers of four cells each are formed, the upper tier of cells being open at the upper side. These eight cells now divide transversely, and four tiers of four cells each, sixteen in all, result. This structure is known as the proembryo.

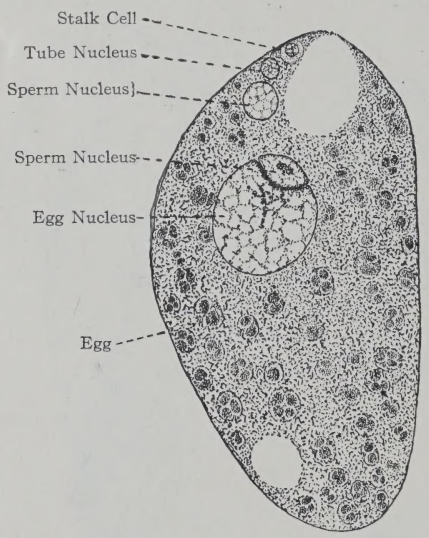


FIG. 406.—*Pinus nigra*. A stage in fecundation, egg and sperm nuclei in contact.

The lowest tier consists of the embryonal cells, the next tier above, the suspensor, and the third tier becomes the rosette. The tier of cells, remaining open above toward the cytoplasm of the zygote, tends to become disorganized.

In the endosperm, just below the archegonia, a narrow, cone-shaped cavity is formed by autodigestion. This cavity is the embryonal path.

The suspensor cells now rapidly elongate, pushing the embryonal cells down toward the center of the endosperm (Fig. 407). As the suspensor elongates, its cells and the four embryonal cells separate, and each embryonal cell begins development into an embryo sporophyte, i.e., an embryo pine tree. Fig. 408 is a proembryo dissected out of the endosperm. The long suspensor cells, now much curved, have separated, freeing the four embryonal cells, which have given rise to the four young embryos, e^1, e^2, e^3, and e^4. From every fecundated egg in Pinus, therefore, at least four

embryos begin development. In some cases embryos may also begin to develop from the rosette.

It frequently happens that two or more eggs are fecundated, and, as a consequence, many embryos may begin development in the ovule. Owing

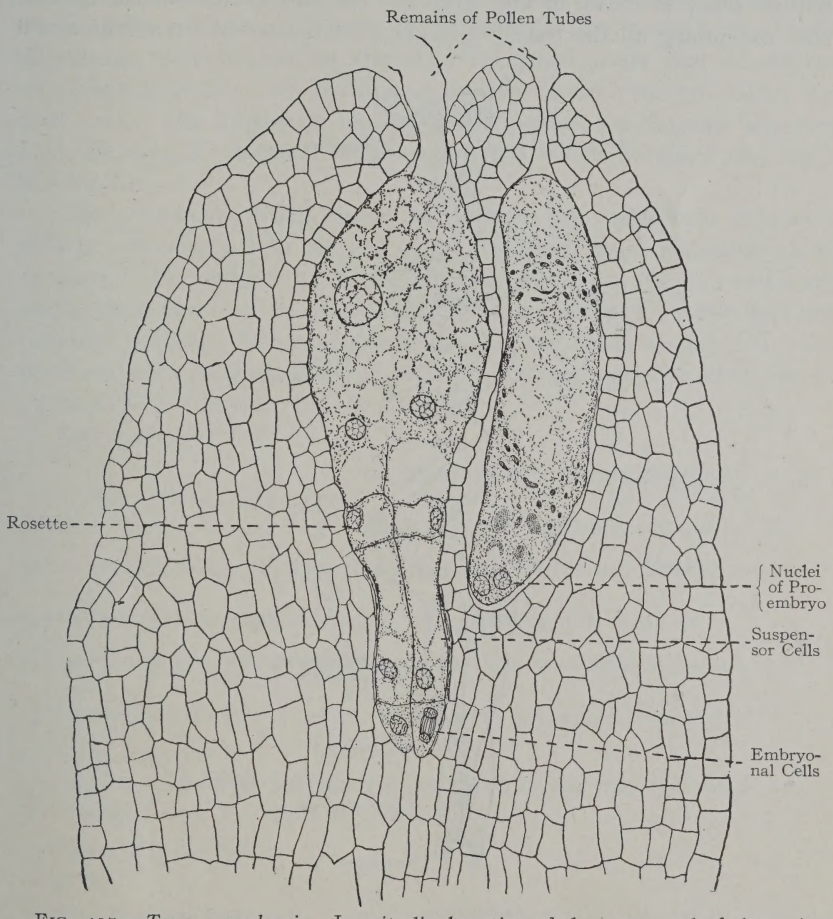


FIG. 407.—*Tsuga canadensis.* Longitudinal section of the upper end of the endosperm, showing two zygotes with proembryos in different stages of development. In the zygote at the right the proembryo consists of four nuclei at the bottom, two being shown. In the zygote at the left the proembryo consists of the embryonal cells, the suspensor, the rosette, and four cells above open on the side next to the cavity of the zygote.

to competition among them, only one, as a rule, survives to the maturity of the seed. In some cases two embryos develop in a seed, one being usually a little larger than the other. In *Pinus edulis*, four or five embryos of varying sizes have been found in one seed.

In many gymnosperms the embryonal cells do not separate, and only one embryo develops from one fertilized egg.

Maturing Cone and Seed.—During the remainder of the summer following fecundation, the embryo gradually develops to that of the mature seed, as shown in Fig. 393, A. The endosperm also increases in size, consuming all the nucellus except a small, cap-like remnant at the

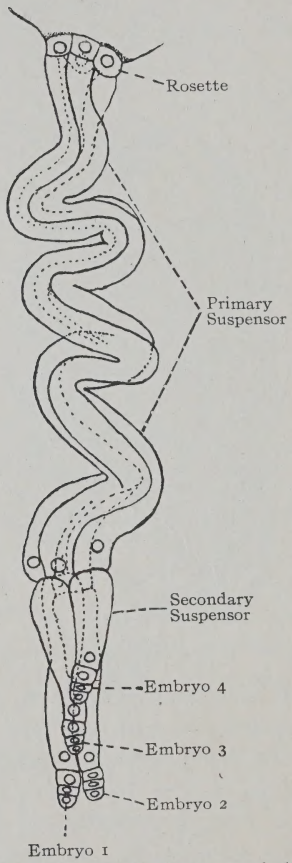


FIG. 408.—*Pinus nigra*. Proembryo dissected out of the endosperm. The separation of the suspensor cells have isolated the four potential embryos. (After Buchholz.)

micropylar end. The larger outer part of the integument becomes stony tissue. An inner and softer layer of the integument becomes the thin, separable, papery, brown membrane surrounding the endosperm.

A thin layer of tissue splits off the adaxial face of the ovuliferous scale to form the wing of the seed. The ovuliferous scales become brown, dry, and bony. The entire vegetative part of the cone now represents dead

tissue, the embryo and endosperm being the only living parts. If a mature cone be cut in two, as in Fig. 398, C, the seeds, each containing an embryo, may be seen in position.

Germination of the Seed.—Pine seeds may germinate readily the spring following their liberation from the cone, and many retain their viability for a number of years. Supplied with the necessary conditions of warmth, moisture, and air, the seeds will absorb water, and the embryo will begin growth. The swelling of endosperm and embryo bursts the seed coat. The hypocotyl elongates and pushes out through the seed coat, bending if necessary so that the root which develops may grow downwards.

The cotyledons, which digest and absorb the endosperm, gradually enlarge and emerge from the seed coat. By the time the endosperm is all consumed, the embryo has freed itself completely from the seed coat, and germination is at an end. The cotyledons persist for some time and function as foliage leaves until secondary leaves are developed. In some pines the embryo becomes green before it emerges from the seed; that is, chlorophyll will develop here in darkness.

Life cycle of Pinus:

Sporophyte (pine tree) (2x) → staminate cone (2x) —microsporangium (2x) → (*a*)
Sporophyte (pine tree) (2x) → ovulate cone (2x) —megasporangium → (*b*)

(*a*) → (pollen sac)—microspore (2x) mother cell—reduction division →
(*b*) → (ovule)—megaspore (2x) mother cell—reduction division →

(*a*) → microspore (x) (pollen spore)—pollen tube (parasitic in ovule) (x) →
(*b*) → megaspore————————endosperm (parasitic in ovule) →

(*a*) → sperm (x)
(*b*) → egg (x) → embryo sporophyte (2x) (parasitic in endosperm)—adult →

sporophyte (pine tree).
(2x)

The Foliage Leaf.—In many conifers, the foliage leaves are inserted singly on the shoot, but, in the pines, they are borne in groups, or fascicles, on dwarf shoots of limited growth. The two needles in each cluster, in *Pinus nigra*, are semicylindrical in form, with the flat surfaces facing each other. Longitudinal rows of minute whitish dots indicate the position of stomata.

In a cross section is seen a central vascular region (stele) surrounded by a definite layer of cells, the sheath (Fig. 409, B). In this region are two vascular bundles, the xylem of each facing the flat (adaxial) side of the

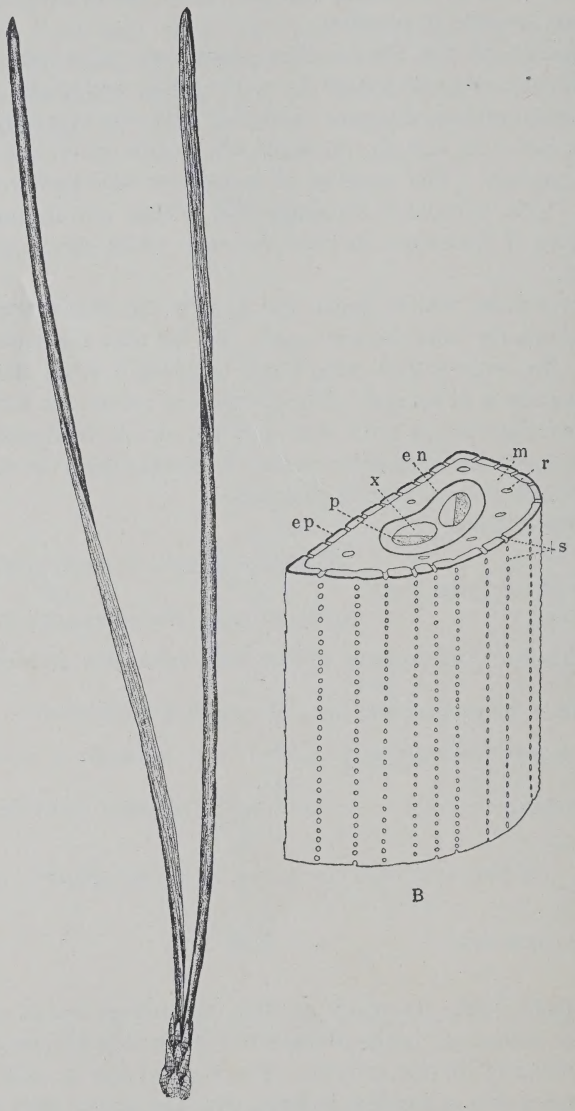


FIG. 409.—*Pinus nigra*. A, dwarf shoot bearing two foliage leaves ("needles"). B, portion of a leaf, enlarged, the cross section shown in diagram. *ep*, epidermis; *p*, phloem; *x*, xylem; *en*, endodermis; *m*, mesophyll; *r*, resin duct; *s*, stomata.

leaf. Surrounding the central region is the green mesophyll, whose cells have peculiar infoldings on their walls, thus increasing the surface over which the chloroplasts are distributed. Many intercellular spaces are present (Fig. 410). In the mesophyll are resin ducts, each surrounded by a layer of resin-secreting cells, and these in turn surrounded by a layer of thick-walled cells. The epidermal cells are thick-walled, the outer walls possessing a thick outer layer of cutin. The stomata lie at the bottom of depressions, and below each stoma is a large intercellular space. Below the epidermis is a region of cells with very thick, silvery white walls, whose cavities are connected by narrow pits.

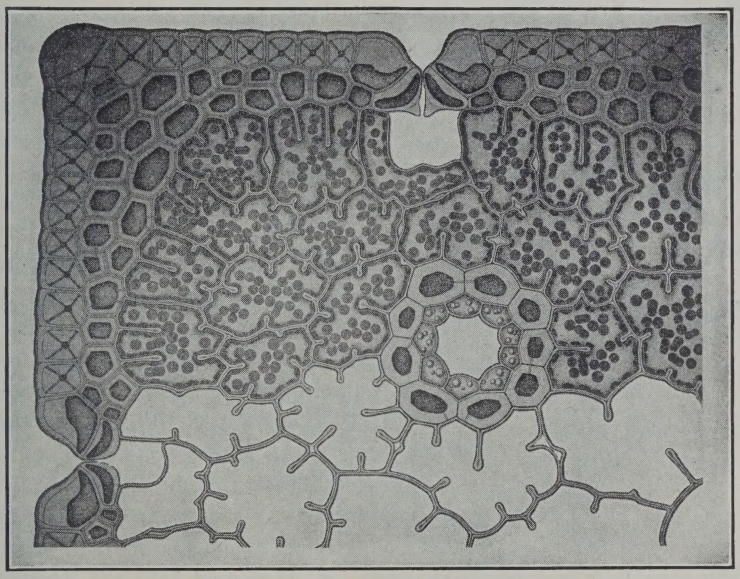


FIG. 410.—Cross section through corner of a foliage leaf, or needle, of Pine. (From Kny's Chart.)

The very striking contrast in appearance between the evergreen conifers and the broad-leaved deciduous forest trees is due to the scale-like, awl-shaped, or needle-shaped leaves and the very dark green color of the foliage. These leaves are well adapted to the severe conditions of a winter climate. The needles of the pines and others, and the small, closely fitting scale-like leaves borne by the slender twigs of the arbor-vitae and red cedar present the minimum surface both for the accumulation of snow and for transpiration. Winter climate, as regards trees, is a very dry or xerophytic one, for the reason that the trees are able to absorb comparatively little water from the cold or frozen soil, and because of the

fact that alternate freezing and thawing of parts exposed to the air constitute a drying process in so far as vegetation is concerned. As an adaptation to this and other xerophytic conditions, the epidermal cells have thick walls, with a rather thick layer of cutin on the outside. The stomata are deep-set, and beneath the epidermis are one or more layers of thick-walled cells. The entire leaf surface is consequently provided with effective water-proofing.

FIG. 411.—A small branch of Arbor Vitae (*Thuja*). Note the small woody cones and the over-lapping scale-like foliage leaves. (After Eichler.)

Moreover the mesophyll of the needle is very rich in chloroplasts which accounts for the deep green color. In short the pine needle represents a large quantity of photosynthetic tissue done up into a small package. The bronzing of the leaves of cedars, etc., in winter is partly due to the change of the reserve food from carbohydrate to oil.

Certain varieties of arbor-vitae especially have a very light yellow or golden color.

Some Common Gymnosperms.—Among our common evergreen trees are the arbor-vitae or white cedar (Thuja) (Fig. 411), the red cedar (Juniperus) (Fig. 412), the hemlock (Tsuga), the spruce (Picea) and the fir (Abies). In these, one year only is necessary for the development of the seed. In the red cedar the very small ovulate cone, consisting of a few carpels, is developed into the drupe-like fruit, the "cedar berry." In the development of this "berry" the carpels are transformed into the dry pulp-like tissue which encloses the one or more seeds. The fruits are often eaten by birds. The larch, or tamarack (Larix), and the bald cypress (Taxodium) are deciduous.

CLASSIFICATION OF GYMNOSPERMS

All gymnosperms known to botanical science, both living and extinct, are included in seven great groups: (1) Cycadofilicales, (2) Bennettitales, (3) Cycadales, (4) Cordaitales, (5) Ginkgoales, (6) Coniferales, and (7) Gnetales.

1. **Cycadofilicales.**—The Cycadofilicales, sometimes referred to as the seed-bearing ferns, have no living representatives. Our knowledge of the group is based upon fossil remains found only in the Paleozoic, chiefly in the Pennsylvanian deposits. The coal measure deposits are rich in the remains of fern-like plants, which constituted about one-half of the vegetation of that time.

FIG. 412.—Branch of the Juniper, *Juniperus communis*. The branch at the left bears staminate cones; that to the right bears ovulate flowers (cones) above and mature cones below, which have matured into the drupe-like fruit. (After Berge and Schmidt.)

The sporophyte was strikingly fern-like, including not merely the usual fern habit, but also climbers and tree-like ferns. The seeds were borne at the margin of the foliage leaves, although in certain forms these differed somewhat from the purely vegetative leaves (Fig. 413). In such cases the seeds terminated naked branches and were often surrounded by a husk-like cover or cup. The microsporangia were similar to those in

ferns. In general the ovules resembled those of the pines. It is doubtful whether pollen tubes were developed from the microspores. Surrounding the tip of the nucellus was a circle of cavities capable of holding water, in which the microspores were deposited at the time of pollination. The microgametophyte may have borne some resemblance to that of such water ferns as Salvinia or Azolla. In all probability motile sperms were present, swimming into the egg after the disorganization of the nucellar tissue above the archegonia.

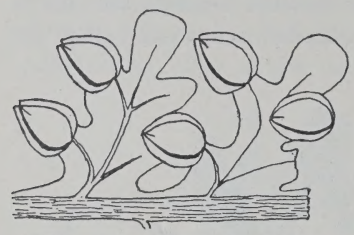


FIG. 413.—*Pecopteris pluckeneti.* Two pinnules of leaf bearing seeds at ends of veins. (From Zeiller, after Grand'Eury.)

2. **Bennettitales.**—This extinct group, usually referred to as the fossil cycads, flourished during the Mesozoic, or age of Cycads. They were abundant during Jurassic time, numerous remains having been found in Maryland, South Dakota, and other parts of northern North America, as well as in Europe and Asia.

FIG. 414.—*Cycadeoidea dacotensis.* Fossilized stem. (From Wieland.)

The stem of the sporophyte was usually a short, stocky, or tuberous body, resembling the stem of certain living cycads (Fig. 414). It bore a crown of large fern-like leaves. The stem was covered with an armor of leaf bases, from among which sprang short axillary branches bearing terminal strobili (Fig. 414). The strobili were bisporangiate, a condition

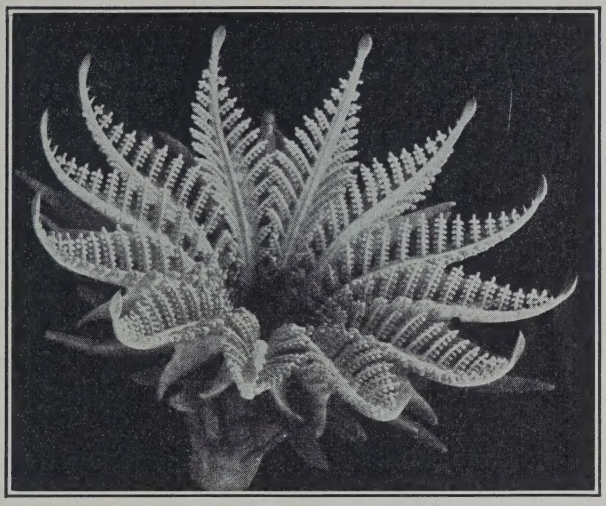


FIG. 415.—*Cycadeoidea ingens.* Photograph of a flower restored in glass at the Field Columbian Museum, Chicago, on the basis of the Yale specimens. (From G. R. Wieland.)

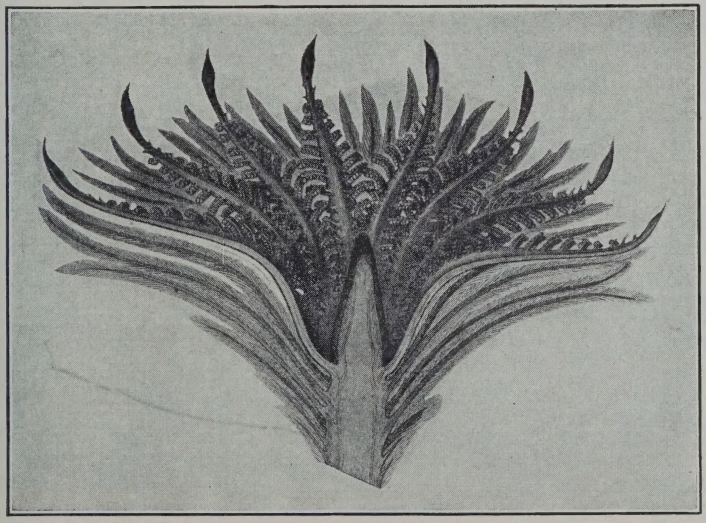


FIG. 416.—*Cycadeoidea ingens.* Restoration of an expanded strobilus in median longitudinal section. (From Wieland.)

FIG. 417.—*Zamia floridana.* A pot-grown specimen with ovulate cone ready for pollination.

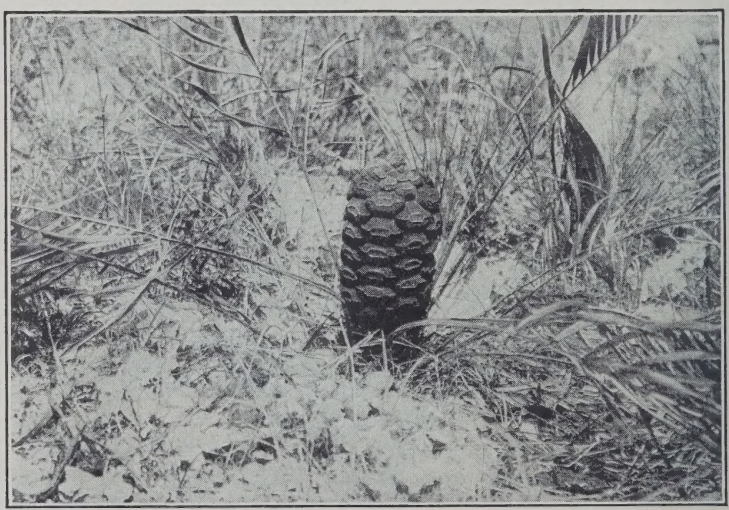
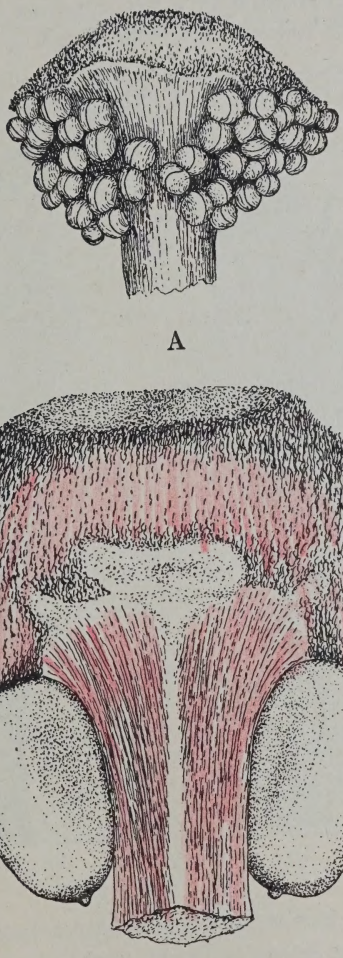


FIG. 418.—Zamia floridana. Fruiting plant in its native habitat near Homestead, Florida. As the seeds mature, the foliage leaves tend to die. (Photo. by P. Weatherwax.)

rarely occurring among living gymnosperms. When the strobili were expanded at the time of shedding the pollen, they bore some resemblance to the flower of higher plants (Figs. 415, 416). The megasporophylls were borne on an axis resembling the conical mass of carpels in a Magnolia



A

B

FIG. 419.—*Zamia floridana*. A, microsporophyll seen from abaxial side. B, megasporophyll.

blossom. The compound microsporophylls bore a striking resemblance to the leaves of certain ferns and produced numerous synangia.

3. **Cycadales.**—The living cycads are confined to tropical or subtropical regions. About 100 species have been listed. Of the nine genera,

Cycas and Zamia are most commonly encountered, species of the latter being native to southern Florida.

The columnar stem of Cycas bears a crown of large, leathery, pinnate leaves at the top, which alternate in order of development with a crown of short scale leaves covered by a felt of brown hairs; that is, a crown of foliage leaves will be followed in development by a crown of scale leaves.

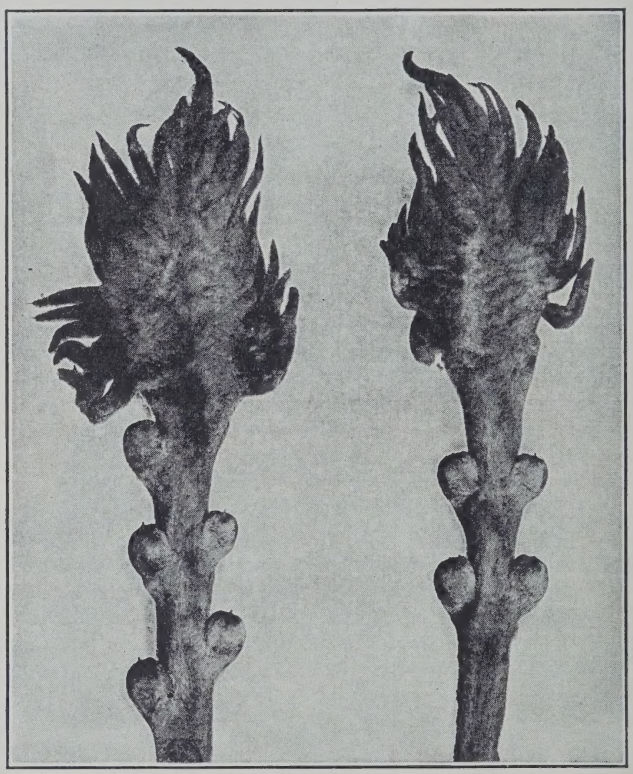


FIG. 420.—*Cycas revoluta.* Two megasporophylls. Note the pinnate character of the ends of the sporophylls.

The tuberous stem of Zamia, which is mostly subterranean, bears also a crown of similar foliage leaves (Figs. 417, 418).

Staminate Strobilus.—The staminate and ovulate strobili of Zamia are quite similar in external appearance. Each microsporophyll bears two groups of microsporangia on the abaxial side (Fig. 419, A). Each megasporophyll bears two megasporangia (Fig. 419, B).

The staminate strobilus of Cycas is a large, compact, structure, bearing numerous long, epaulette-like sporophylls, which bear numerous sporangia on the lower side.

Ovulate Strobilus.—The ovulate cone of Cycas is not a compact strobilus, but a loose rosette of megasporophylls resembling reduced foliage leaves covered with a felt of stiff tawny or brown hairs. The ovules are borne on the lower pinnae, two or more on each side. The ovules seem to replace the pinnae completely (Fig. 420).

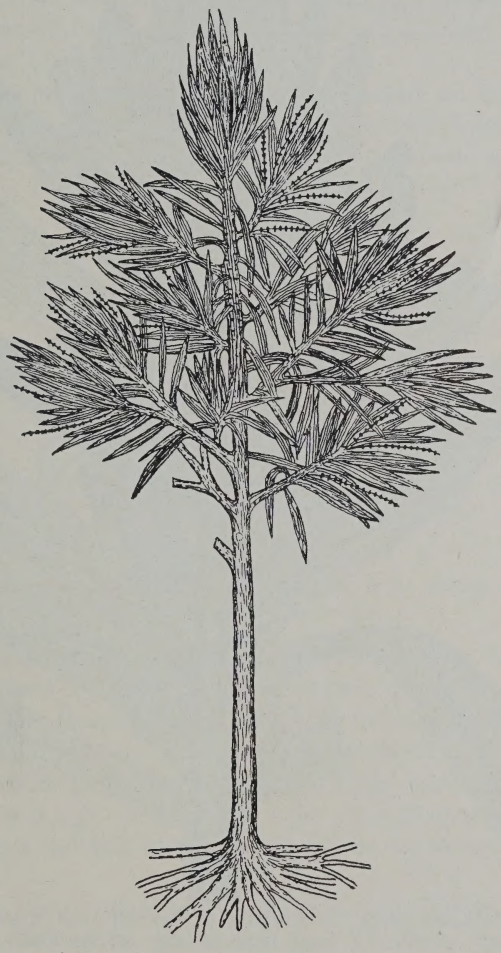


FIG. 421.—Dorycordaites. Restoration (reduced) of a tree, showing roots, trunk, and crown of branches bearing large lanceolate leaves and inflorescences. (From Grand'Eury.)

Motile sperms are developed in the pollen tube of the Cycadales. The basal end instead of the tip of the tube grows towards the archegonium and discharges the sperms above the neck of the archegonium in a depression at the micropylar end of the endosperm. The distal end of the

pollen tube, which takes in general a transverse direction in the nucellus, acts as a haustorium, or food absorber, while in the pine and distal end of the tube carries the sperm nuclei to the egg.

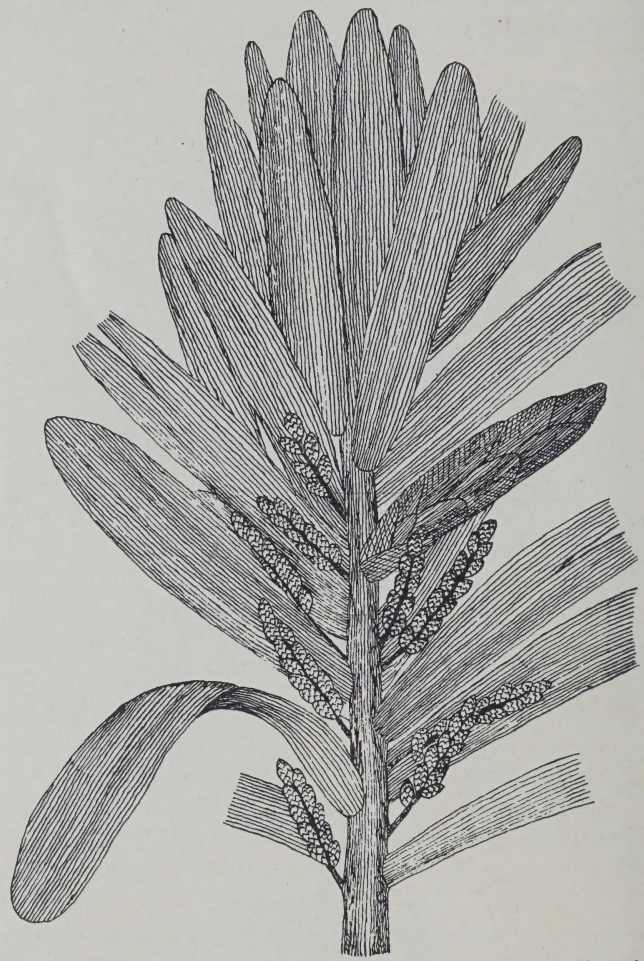


FIG. 422.—*Cordaites laevis*. Restoration of branch with spatulate leaves, and bearing numerous strobili; a large bud is seen at the right. (Adapted from Grand' Eury.)

In the mature seed of Cycas, Zamia, and other genera, the external part of the integument develops into a soft, pulpy, orange-colored layer, while the inner part becomes stony.

4. **Cordaitales.**—Like the Cycadofilicales and Bennettitales, the Cordaitales represent an extinct group of gymnosperms. Their fossil remains

occur in the Paleozoic deposits, and it is possible that they constituted the dominant forest type of gymnosperms at that time. They occurred side by side with the Cycadofilicales as far back as the records go. Intergrading forms seem to indicate that the Cordaitales probably arose from the Cycadofilicales at a very early period.

They were tall, slender trees, often attaining a height of 30 meters, bearing a crown of large, simple, and rather broad leaves. A restoration is shown in Fig. 421.

The flowers, which occur in catkin-like clusters on lateral branches, are small and monosporangiate, as is the case of the Coniferales (Fig. 422). Both kinds are borne on the same tree, hence the sporophyte is monoecious.

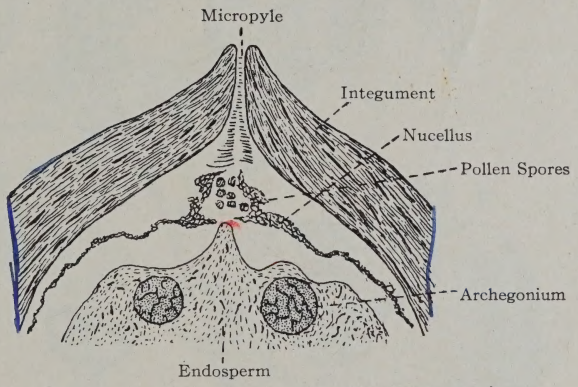


FIG. 423.—*Cycadinocarpus angustodunensis.* Longitudinal section of upper part of ovule. (From Renault.)

The staminate catkin consists of spirally arranged bracts, between which the stamens are inserted. Each stamen consists of a filament bearing three or more terminal pollen sacs. The ovulate catkin is similar to the staminate. The ovule bears a striking resemblance to that of Ginkgo (Fig. 423). Pollen grains are preserved in large quantities. Each seems to have contained a group of internal cells. Motile sperms were probably present, but it is doubtful whether a pollen tube was developed as in living gymnosperms.

Neither in the Cordaitales nor in the Cycadofilicales have embryos been found in the remains of the seeds.

5. **Ginkgoales.**—This group is represented by one living species, *Ginkgo biloba*, commonly known as the Ginkgo tree, or maidenhair tree. Its ancestry has been traced back to the Cordaitales. The Ginkgoales were probably abundant in the Mesozoic. The tree, whose leaves resemble the leaflets of the maidenhair fern (Fig. 424), is now extensively cultivated, since it thrives well in temperate regions.

For many years it has been extensively cultivated by the Chinese and Japanese, especially in their temple grounds. For a long time it was supposed that the tree did not exist in the wild state. In recent years

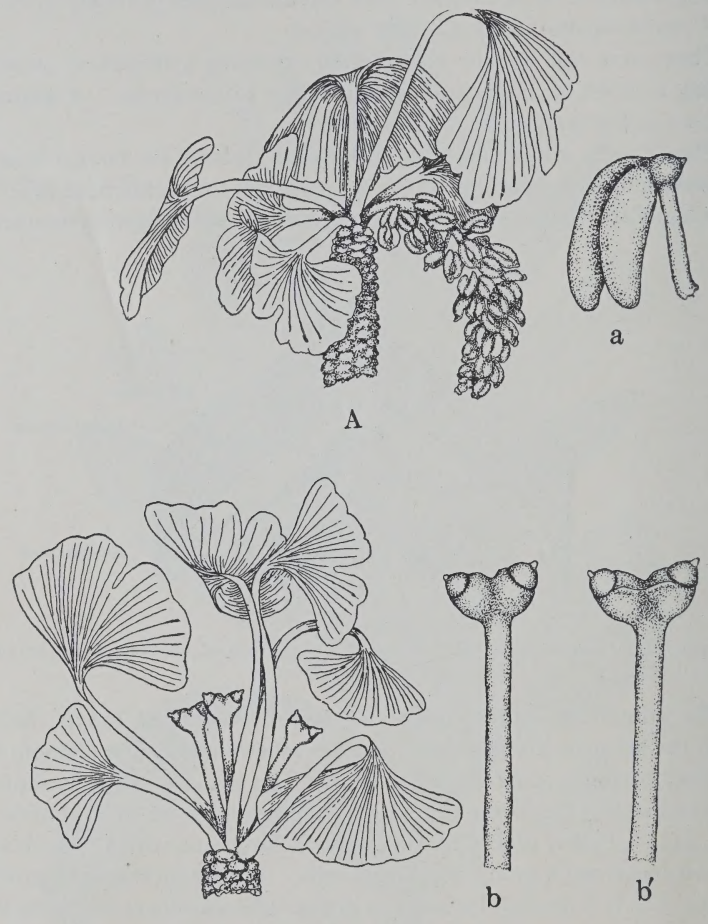


FIG. 424.—*Ginkgo biloba*. A, twig with leaves and staminate inflorescence; *a*, one microsporophyll. B, twig with leaves and ovulate inflorescence; *b*, megasporophyll with two ovules, seen from the under (abaxial) side; *b′*, the same as seen from the upper (adaxial) side.

specimens have been reported as growing wild in the mountains of western China.

The Staminate Flowers.—Opinions differ as to whether the flowers of Ginkgo are to be regarded as strobili or merely as sporophylls of a more primitive character. The staminate and ovulate flowers occur on different

trees, hence the sporophyte is dioecious. The staminate flowers are catkin-like structures borne at the ends of short branches (Fig. 424, A). Each stamen consists of a very short stalk from near the end of which two (sometimes more) pendent, sack-like sporangia are borne (A, *a*).

The Ovulate Flowers.—The ovulate flowers are borne also at the ends of short branches. Each flower consists of a long, slender stalk, near whose tip, as a rule, two megasporangia are borne (B, *b*, *b'*). One of these usually matures. At the base of each ovule is a little collar.

The ovule is similar in structure to that of Zamia. The distal end of the pollen tube, as in the Cycadales, becomes a haustorium, while the

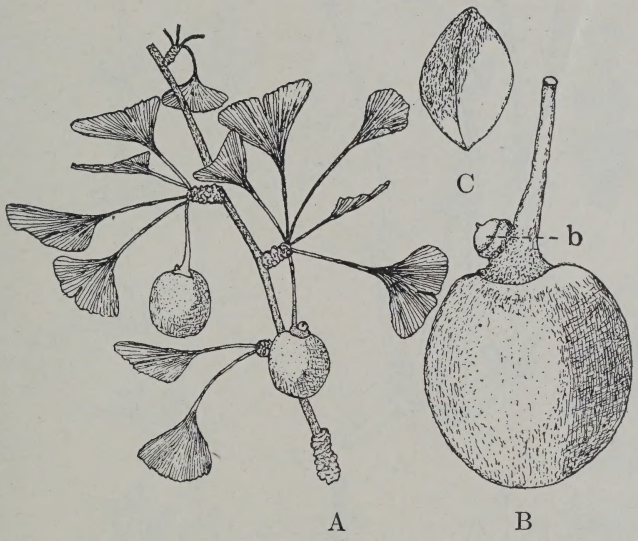


FIG. 425.—*Ginkgo biloba*. A, portion of branch with two mature seeds. B, mature seed, natural size; *b*, aborted ovule. C, seed, with pulp removed. (After Bailey.)

two motile sperms are developed in the basal end, which grows towards the archegonium and discharges the sperms.

The seeds, as they hang on the tree, resemble green plums (Fig. 425). The seed coat, as in the Cycadales, has an outer pulpy layer and an inner stony layer. The embryo has two cotyledons, one of which may be lobed.

6. *Coniferales.*—This is the largest group of gymnosperms, including the vast majority of commonly known evergreens, such as pines, spruces, junipers, firs, hemlocks, arbor-vitae, cedars, Sequoias, yews, tamaracks (larches), bald cypress, etc.

Two large families are recognized, the Taxaceae and the Pinaceae.

Taxaceae.—The Taxaceae, in general, have fleshy coated seeds and freely exposed ovules. There are about 11 genera and 100 species. Taxus (the yew tree) and Podocarpus are representative genera.

Pinaceae.—The Pinaceae have, in general, dry seeds borne in woody cones, as in Pinus and others.

The "cedar berry" of the red cedar, or juniper, represents a very small transformed cone, the carpels of which have grown together to form a thin pulp surrounding the bony seed or seeds.

The Pinaceae comprise 29 genera and 250 species.

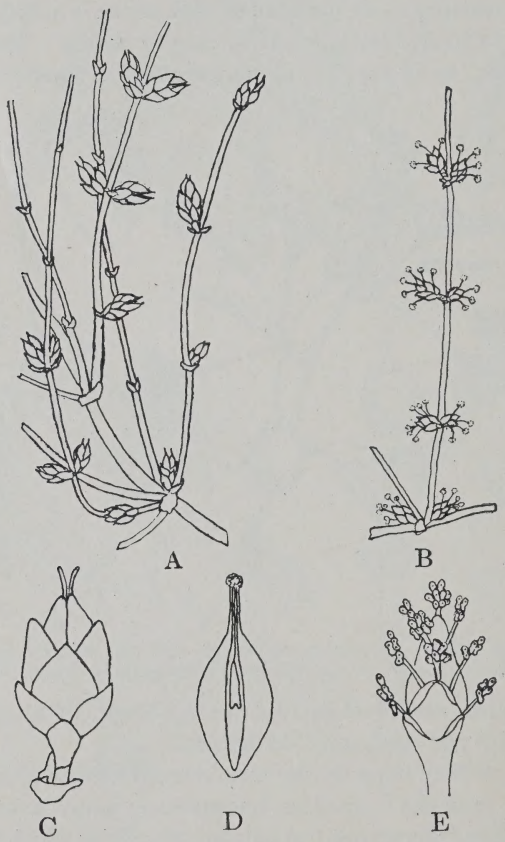


FIG. 426.—Ephedra. A, branches with ovulate strobili. B, branches with staminate strobili. C, ovulate strobilus. D, an ovulate flower. E, staminate strobilus with staminate flowers in the axils of bracts. (From Watson.)

7. *Gnetales.*—The Gnetales, the most highly developed of the gymnosperms, are confined to tropical or subtropical regions, although a number of species occur in the temperate zone. They are of special interest because of the resemblance of many of them to the angiosperms, both in habit and anatomical structure, and in the flowers (strobili), which suggest

strongly the inflorescence of certain dicotylous plants. Three genera are recognized: Ephedra, Welwitschia (Tumboa), and Gnetum.

Ephedra.—This genus includes about 50 species. In a species found in Arizona the sporophyte is a switch-like plant, with long, jointed, green, fluted stems. At each joint two scale-like leaves are borne (Fig. 426). The strobili are borne at the nodes and resemble the inflorescences of certain angiosperms.

Staminate Strobilus.—A staminate "flower" consists of an axis, bearing at its top two or more sporangia (Fig. 426, E). These flowers arise in the axils of the bracts of the strobilus.

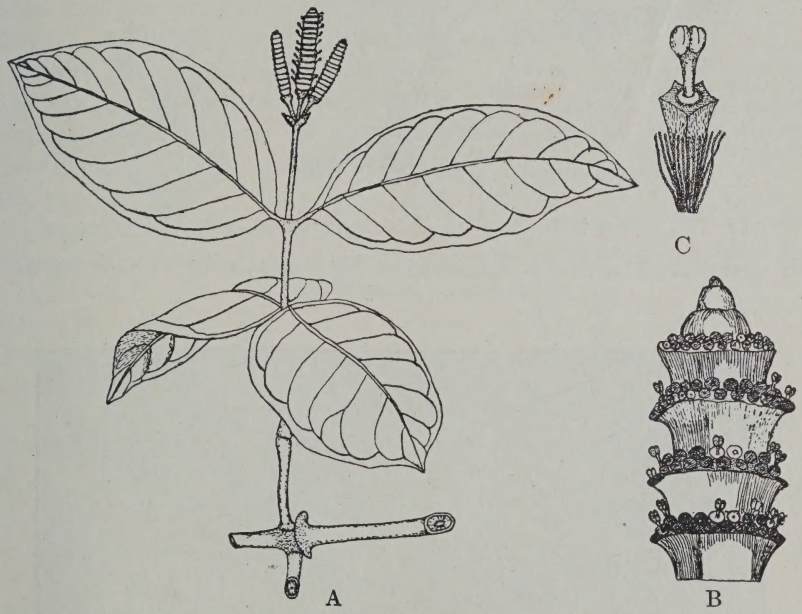


FIG. 427.—*Gnetum latifolium.* A, branch bearing staminate strobili and foliage leaves. B, portion of staminate strobilus with staminate flowers in the axils of the "connate" bracts. C, a single staminate flower. (From Blume.)

Ovulate Strobilus.—The ovulate strobilus is similar to the staminate. The ovule has two so-called integuments, as in Gnetum and Welwitschia, the inner forming a long, tube-like micropyle (D). The megagametophyte (endosperm) corresponds to the usual gymnospermous type, the larger part of it being formed before fecundation, and archegonia are present.

Gnetum.—In Gnetum the sporophyte may be a small tree or a woody climber. The leathery, opposite, net-veined leaves resemble those of certain dicotylous angiosperms (Fig. 427, A).

Staminate Strobilus.—In the staminate strobilus the connate bracts, in whose axils the "flowers" are borne, form a series of contiguous, but

not overlapping, cups placed one above another on the axis (B). Each staminate flower consists of an axis bearing two microsporangia (in

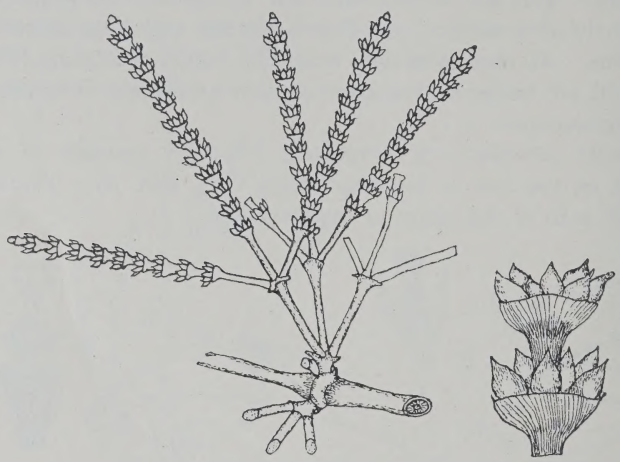


FIG. 428.—*Gnetum latifolium*. A, branches bearing ovulate strobili. B, part of ovulate strobilus. (From Blume.)

FIG. 429.—*Welwitschia mirabilis* in its natural surroundings (from a sketch by its discoverer). (From Kerner.)

Gnetum latifolium) at its upper end (C). This axis is surrounded at its base by a tube of coalesced bracts which form a sort of perianth, a structure resembling in some respects a calyx.

Ovulate Flowers.—The ovulate strobili have the same general make-up as the staminate (Fig. 428). The ovule has two integuments, and it is surrounded by a kind of perianth similar to that of the staminate flower.

In the development of the seed, Gnetum differs widely from the gymnospermous type in two very important ways, namely, in the absence of archegonia and in the development of the bulk of the endosperm after fecundation. At the time of fecundation the endosperm, in some species at least, consists merely of a layer of cytoplasm in its large upper part, in which are many free nuclei, and a small amount of cellular tissue in its lower, chalazal, end. The egg lies among the free nuclei in the upper part of the endosperm.

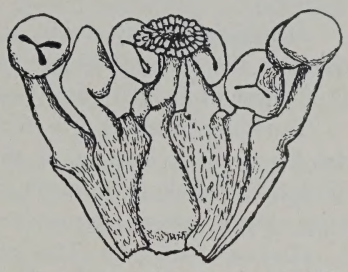


FIG. 430.—*Welwitschia mirabilis.* Staminate flower, showing six stamens united below, and a sterile ovule with twisted micropylar tube; each stamen bears three sporangia. (Adapted from Hooker.)

Welwitschia.—The sporophyte of Welwitschia has a large, woody body shaped like a turnip or sugar beet, from whose flattened crown are borne

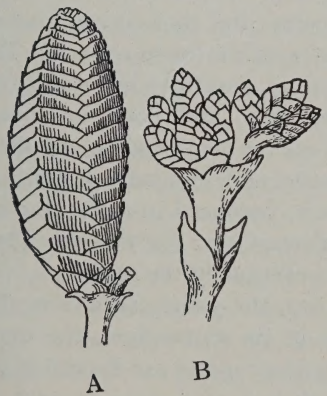


FIG. 431.—*Welwitschia mirabilis.* A, ovulate strobilus. B, a branch bearing staminate strobili. (From Hooker.)

FIG. 432.—*Welwitschia mirabilis.* Longitudinal section of an ovulate flower showing the surrounding winged bracts, the two integuments, and the nucellus containing the megaspore; the micropyle is formed by the inner integument. (Modified from Strasburger, Macmillan Co.)

two long, straggling, strap-shaped, parallel-veined leaves. These two leaves persist throughout the life of the plant (Fig. 429). The cone-shaped

strobili are borne at the edge of the crown of the stem. Only one species (*Welwitschia mirabilis*) is known. It occurs in the arid districts of western south Africa, and is one of the most remarkable plants known to science.

Staminate Strobilus.—In the staminate strobilus the "flowers" are borne in the axils of the bracts (Fig. 431, B). These differ considerably from those of Ephedra and Gnetum.

The flower consists of a circle of six stamens united at the base (monadelphous), each bearing at the upper end three sporangia (Fig. 430). Within the circle of stamens is a single terminal aborted ovule, with its long, spirally coiled micropylar tube, which ends in a broad, flaring tip.

Ovulate Strobilus.—The ovulate strobilus has the same general make-up as the staminate (Fig. 431, A). The ovule has two integuments and is surrounded by bracts resembling a perianth (Fig. 432). A set of rudimentary "stamens" doubtless appears outside the ovule.

Among fossil gymnosperms the close association of functional stamens and carpels is found only in the Bennettitales. It seems reasonable to suppose that the staminate flower of Welwitschia may have arisen through the abortion of the ovule, and the ovulate flower by the abortion of the stamens.

Summary.—1. In the Gymnosperms the sporophyte (diploid structure) attains the size of the largest trees known to science. The sporophyte bears seeds, two kinds of branches, and three kinds of leaves. The three kinds of leaves are foliage, scale, and floral or spore-bearing leaves. The two kinds of branches are the *long branches* of indeterminate or unlimited growth, and *dwarf branches* of determinate or limited growth.

2. There are two kinds of flowers, produced in cones, the staminate and the ovulate. The staminate flowers bear the pollen. The ovulate flowers produce the megaspores and eventually the seeds.

3. Of the two kinds of spores, one, the pollen, falls from the flower; the other, the megaspore, remains in its sporangium, the ovule. The ovule is pollinized when a pollen spore or spores are deposited in or near the micropyle.

4. The two kinds of spores give rise to the two gametophytes (haploid structures). The pollen spore produces the male gametophyte, the pollen tube. The megaspore gives rise to the female gametophyte, which we now call endosperm. Both pollen tubes and endosperm live parasitically in the ovule, strictly speaking in the nucellus; they are parasites but not pathogenes.

5. In the Coniferales and Gnetales the pollen tube bears two sperm nuclei; in the Cycadales and in Ginkgo, two or more motile sperm cells. In the Coniferales and Gnetales the distal end of the pollen tube grows to

the egg, opens and discharges all of its contents into the egg. In the Cycadales and in the Ginkgoales the basal or proximal end of the pollen tube grows towards the archegonia and discharges its contents above them, the distal end of the tube functioning as an haustorium. One sperm nucleus unites with the egg nucleus. This constitutes fecundation.

6. In the pine, four or more embryos begin development from each fecundated egg, but only one, as a rule, survives. Usually the mature seed has but one embryo.

7. During the maturing of the seed the embryo develops a large hypocotyl with the beginning of the root, and the cotyledons. The endosperm consumes and replaces the nucellus with the exception of a small portion at the micropylar end. The integument of the ovule matures into the seed coat, which, in the majority of Gymnosperms, has two easily visible and readily separable layers, the hard stony shell and the thin, brown, papery membrane. In the Cycadales and in Ginkgo the seed coat becomes differentiated into an outer pulpy or fleshy layer which surrounds the stony layer. The seed coat and the cone become dead tissue; the embryo and endosperm are the only livng parts.

8. From the evolutionary standpoint we find the outstanding facts in comparing a gymnosperm with the highest Pteridophyte:

a. In the Pteridophyta both microspores and megaspores are eliminated from the sporophyte. The gametophytes develop as independent individual plants in the water or upon the soil, even though supplied with stored food.

b. In Gymnosperms only the microspores are shed from the sporophyte, the megaspore remaining in the sporangium. Both gametophytes are parasitic upon the sporophyte.

c. In the highest Pteridophyta the nearest approach to a seed consists of the embryo with its surrounding gametophyte (Selaginella) which corresponds to the endosperm. In Selaginella there is no seed coat, and the embryo cannot pass into the dormant state, but it must continue development until it is attached to the soil. It cannot dry out and live. In a seed, on the contrary, the embryo may lie dormant for a long time in the dry state. This is the reason that seed plants are better adapted to dry land conditions, and because of this fact seed plants constitute the dominant vegetation of the Earth. Had there been no large dry land areas, would seed plants have been evolved?

TOPICS FOR REVIEW AND DISCUSSION

What does the carpel of Pinus lack of being a pistil like that in angiosperms?
What is a strobilus?
How often does a pine tree produce a crop of new leaves?
How many kinds of leaves are borne by a pine tree?

In what two ways may you know the age of a pine twig?

What are branches of determinate growth? Of indeterminate growth?

What do the determinate shoots of Pinus bear?

Are the staminate and ovulate strobili flowers?

What does the staminate strobilus contribute to seed development?

What does the ovulate strobilus contribute to seed development?

What is the fruit of the pine tree?

How many years are required for the complete development of the seed in Pinus?

Name the conifers which develop seeds in one year.

What time of the year does the pine tree bloom in your locality?

How much of the season's growth of the pine is present in the winter bud?

What is a resin duct or canal in the pine?

Does resin play an important role in the economy of the pine tree?

What is meant when it is said that a pine foliage leaf (needle) represents a lot of photosynthetic tissue done up in a small package?

Are the foliage leaves of the conifers better fitted to endure winter conditions than broad leaves would be?

What gymnosperms mentioned in the text are deciduous?

After pine trees have attained the age of four or five years they shed leaves every year thereafter. Why are they not called deciduous trees?

Why does winter freezing not kill foliage leaves of pines and hemlocks to any great extent?

Why do old pine trees, especially when not too crowded, develop a flat top instead of continuing conical in shape?

What imparts the bluish color to the so-called Colorado blue spruce?

Why do some juniper trees become somewhat bronze-colored in winter?

Name the parts of a pine ovule at the time of fecundation?

Which part bears the archegonia?

What is the micropyle?

What constitutes pollination in Pinus?

What is the smallest number of embryos which begin development from each zygote of Pinus?

What is polyembryony?

Why is but one embryo, as a rule, found in a mature pine seed?

What is meant by the distal end of the pollen tube? The proximal end?

In which orders of living gymnosperms does the proximal end of the pollen tube grow towards the archegonia?

In which gymnosperms are the sperms motile?

What living gymnosperms resemble the fossil cycads closely?

From what order of extinct gymnosperms is it thought the Ginkgo tree descended?

Where in the United States have the fossil remains of Bennettitales been found?

What is the field of study of a palaeobotanist?

In what respects do the Cycadales and Ginkgoales resemble Pteridophytes?

What evidence would you bring forward to support the view that gymnosperms were evolved from fern-like ancestors?

In what genus of gymnosperms are archegonia unknown?

What gymnosperm bears but two foliage leaves during its entire life of many years? Of what continent is this species native?

What species of Pinus produces the highest grade of soft wood lumber?

What rust (fungal parasite) is very destructive especially to the white pine (*Pinus strobus*).

What measures are taken in the United States to prevent the spread of the parasite?

What parts of the mature seed constitute living tissue?

Where in the United States are species of Zamia native?

How far north in the United States will Cycads survive the winter in the open?

What does Selaginella lack of making a seed?

Give a synonym for the term endosperm. One for the term pollen tube.

Upon what is the endosperm directly parasitic? Upon what is the pollen tube parasitic? Upon what is the embryo parasitic?

What is the difference between carpel and megasporophyll?

Why have the cells formed inside the pollen spore of Pinus been called prothallial cells?

Are the wings of pine pollen really wings? Do they function as a parachute, as a sail, or as an airplane?

Why are so many more staminate than ovulate strobili borne upon pine trees?

What is meant by the expression "prodigality of Nature"?

What is the difference between a monoecious and a dioecious gametophyte and a monoecious and dioecious sporophyte?

What is a synangium?

CHAPTER XIX

SPERMATOPHYTA—ANGIOSPERMS

The Angiosperms are usually referred to as the flowering plants, but we have learned that the Gymnosperms also bear flowers. The most fundamental distinguishing characteristic of the Angiosperms lies in the fact that the carpel or carpels (megasporophylls) develop in such a manner as to form a completely closed cavity or cavities in which the ovules are borne. Such structures are known as *pistils*. In the Gymnosperms, as has already been pointed out, the carpels remain open and flat. Pistils are therefore not formed in Gymnosperms in the sense in which we are using the term. The flowers of Angiosperms are not borne in cones. As in the Gymnosperms, flowers consist of one or more spore-bearing parts *with or without accessory parts*. The accessory parts are those which do not bear spores namely, sepals, petals and receptacle. The petals and sometimes the sepals are often very showy and attractive. The flowers will be given special attention in subsequent paragraphs.

The Angiosperms, the most highly differentiated of all plants, represent the highest evolutional development in the plant kingdom. They are grouped into two great subdivisions, the *monocotyledonous* and *dicotyledonous* plants. In the first subdivision the embryo has one cotyledon, while in the latter, two cotyledons are present.* In the presentation of the life history, a familiar plant, such as the garden tulip, will be taken as a sample.

The Garden Tulip.—The general characteristics of a mature flowering specimen of an angiosperm are well illustrated in the tulip of our gardens, of which there are many varieties.

A complete specimen, the *sporophyte*, consists of an underground stem, the bulb, from the center of which springs an aerial stem, bearing two large and one or more smaller foliage leaves, and terminating in a single large flower (Fig. 433, A).

The bulb, as shown in a longitudinal section, consists of a short, flattened or conical stem which bears roots and the fleshy overlapping scales (leaf bases). Near the base of the aerial stem may be present the beginning of the bud of the following year's growth (Fig. 433, D).

* In some monocotyledonous plants the rudiment of a second cotyledon appears in the development of the embyo.

The Flower.—The flower of the tulip consists of five circles or whorls of modified leaves (Fig. 433, B). The six members of the two outer circles constitute the *perigone* or *perianth.* The three outer divisions of the perianth may be regarded as the calyx, and the three inner, the *corolla.*

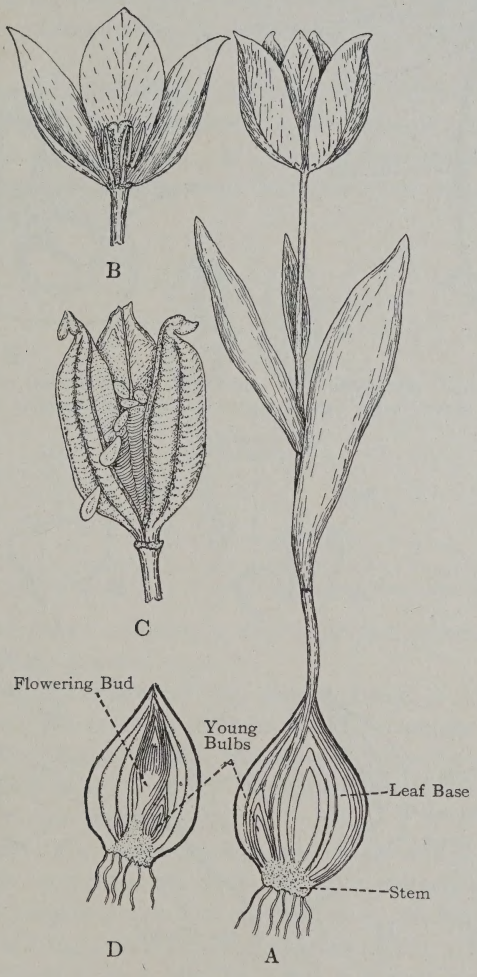


FIG. 433.—The garden tulip, *Tulipa gesneriana.* A, Habit sketch of an entire flowering specimen; the bulb is in section. B, section of flower. C, mature and dehiscent fruit. D, longitudinal section of flowering bulb.

The separate parts of the calyx are the *sepals*, and those of the corolla are the *petals.* The next two circles of three members each are the six stamens (*microsporophylls*). The innermost circle of three members which have developed as one piece constitute the *pistil.* The pistil

represents, therefore, three *carpels* (megasporophylls) grown together. As seen externally the pistil is differentiated into three parts, *ovary*, more correctly *ovulary*, *style*, and *stigma* (Fig. 434, A). In the tulip the

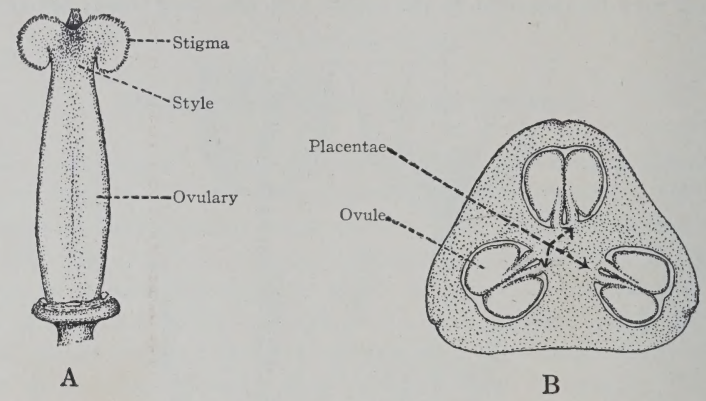


FIG. 434.—*Tulipa gesneriana*. A, pistil. B, cross section of ovulary in outline, showing the three "cells," three placentae, and two rows of ovules in each cell.

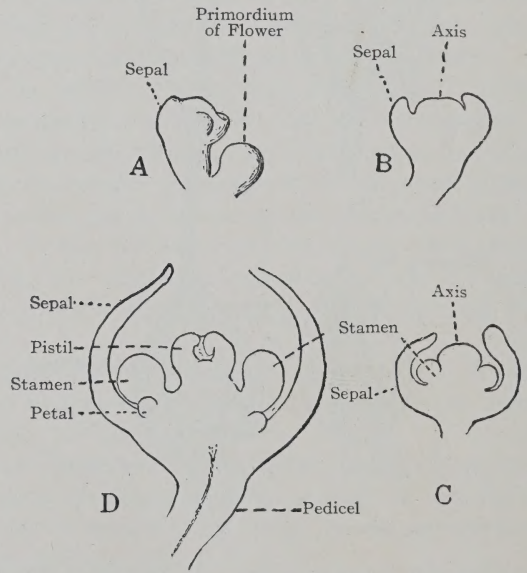


FIG. 434bis.—*Capsella bursa-pastoris*. Stages in the development of the flower.

style, which is very short, ends in a three-lobed stigma. The placenta is the place to which the ovules are attached.

As will be seen in a cross section, the ovulary contains three cavities (Fig. 434, B). In each cavity are two vertical rows of ovules (*megasporangia*). The ovulary of the tulip has three placentae. Each cavity

in an ovulary has long been referred to in descriptive botany as a "cell," and consequently the tulip has a three-celled ovulary. Pistils, like that of the tulip, which are composed of two or more carpels united into one piece, are compound pistils. Compound pistils are recognized as having two or more placentae, two or more "cells" in the ovulary, or two or more styles, stigmas, or stigma lobes. A compound pistil may have but one "cell."

In many flowers as in the larkspur and peony the pistil is composed of one carpel. A pistil composed of one carpel is a simple pistil. A simple pistil is recognized as having *one* stigma, *one* style, *one* placenta and *one* "cell" in the ovulary. In many plants, as in the buttercups (Ranunculus), the flower has several pistils.

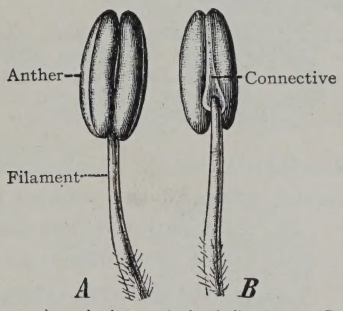


FIG. 435.—Stamens (Hyoscyamus). A, inner (adaxial) view. B, outer (abaxial) view. Dehiscence is longitudinal. (From Strasburger, Macmillan Co.)

All the stamens taken collectively constitute the *androecium;* all the pistils make up the *gynoecium.*

Development of the Flower.—The flower, being a modified stem, appears to the naked eye first as a small bud, and it develops very much as a foliage bud. The flower of the Shepherd's Purse (*Capsella bursa-pastoris*) will serve as an illustration. Several stages in the development are shown in Figure 434 bis, A-D.

The primordium of the flower appears as a minute axis of meristematic cells which enlarges conspicuously into the rounded receptacle and the stalk, which is to become the pedicel of the flower. At four points upon the receptacle the circle of four sepals first appears (A, B). The primordia of the sepals are followed, as a rule, by those of the stamens (C). The pistil arises as a continuous ridge or wall about the apex of the floral axis. The formation of the pistil primordium stops the further growth in length of the floral axis. In Capsella the petals are the last of the floral leaves to appear. They arise upon the axis below the stamens and above the sepals (D). The primordium of the pistil, as seen in Fig. 434 bis, D, will soon differentiate into the bicarpellate, 2-celled structure ending in a

stigma and a very short style. The ovules arise as outgrowths from the placentae. Each stamen primordium develops rapidly into anther and filament. In the flower of Capsella and in those with a similar developmental

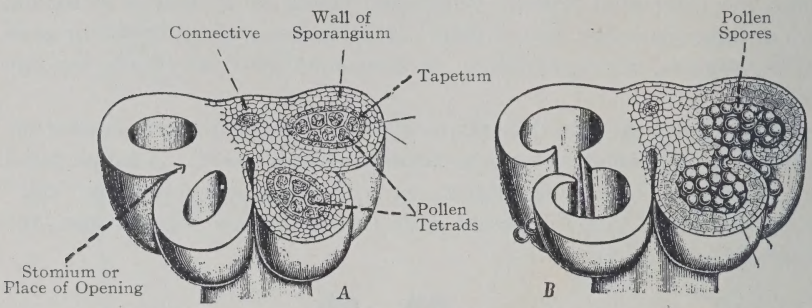


FIG. 436.—Diagramatic cross sections of anthers. A, nearly mature anther, showing the four sporangia, the contents of two having been removed, the other two with spore tetrads. B, mature anther, the pairs of sporangia have merged into the loculi or pollen sacs by the disorganization of the intervening tissue. Dehiscence is longitudinal. (From Baillon's "History of Plants," Librairie Hachette.)

history, it will be seen that the sepals, which develop in advance of the other parts, form a protective cover for the younger parts within. It may be mentioned that the developmental sequence of the different parts of the flower varies in the different types of flowers of which there are many.

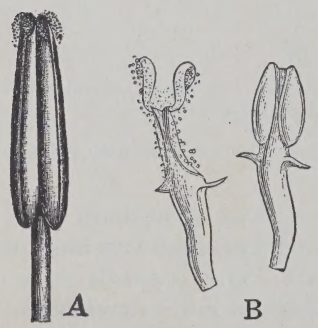


FIG. 437.—Dehiscence of Anthers. A, stamen of Solanum (potato, tomato, night-shade, etc.) opening by pores at the top. B, Berberis, opening by uplifting valves. (From Engler and Prantl.)

The Stamen.—A stamen consists of a slender stalk, the *filament* (Fig. 435), bearing at its upper end an enlarged part, the *anther*. The continuation of the filament into the anther is the *connective*. As a rule the anther consists of four microsporangia, two on each side of the connective, although the number of sporangia in an anther in angiosperms varies from one to several (Fig. 436, A). As the anther matures, the partition, separating the two sporangia of each pair, breaks down and a single cavity, the pollen sac, results (Fig. 436, B). There are, therefore, two pollen sacs to each anther. Each sporangium bears many pollen spores (microspores), and these will be described in a subsequent paragraph.

The anthers open in various ways. In the tulip and lily the opening or dehiscence is longitudinal; in others, as in the May Apple, and barberry, it is effected by up-lifting valves (Fig. 437, B), and in still others by means of pores at the top as in the tomato and certain grasses (Fig. 437, A). A

cross section of an anther opening by longitudinal dehiscence is shown in Fig. 438, A. The cellular partitions between the pairs of sporangia have broken down. The sub-epidermal layer of cells in the anther constitute the mechanical tissue which opens the pollen-sacs.

The Structure of the Young Anther.—The arrangement of the four sporangia is made clear in a cross section of an immature anther of simple structure as shown in Fig. 439. The center of each sporangium is occupied by the microspore mother cells, *pollen mother-cells*. These are surrounded

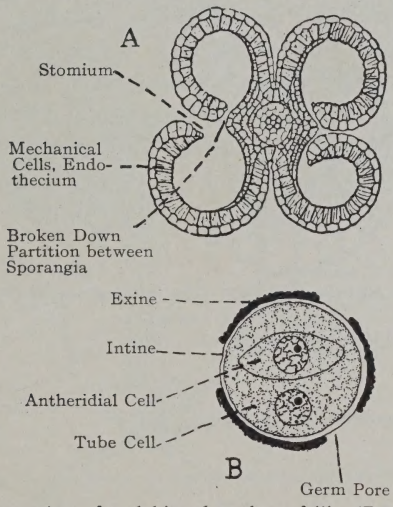


FIG. 438.—A, cross section of a dehisced anther of lily (Butomus). The layer of cells beneath the epidermis acts as mechanical tissue to open the pollen sacs. B, Section of a pollen spore, diagramatic. (A, after Sachs.)

by a layer of nourishing cells, the tapetum. Outside of the tapetum is the wall of the sporangium, consisting of a number of layers of cells. In the tulip and lily the large cells just beneath the epidermis have characteristic band-like thickenings upon the walls. This layer is the *endothecium*, which assists mechanically in the dehiscence of the anther. Opposite the partition between each pair of sporangia, the epidermal cells become characteristically changed and constitute the *stomium*. The stomium marks the line of opening or dehiscence, which in the tulip and lily is longitudinal. As the anther matures, the cellular partition between adjacent sporangia breaks down throwing the two cavities into one, which is known as the loculus or "cell" of the anther (Figs. 436, B, 438, A).

The Pollen Spore.—The mature microspore consists of two cells, one included within the other. The large cell of the spore is the tube cell, and the smaller lenticular or crescentic cell within is the antheridial cell

(designated also as the generative cell) (Fig. 438, B). The antheridial cell is delimited by a plasma membrane only. In some plants the anther-

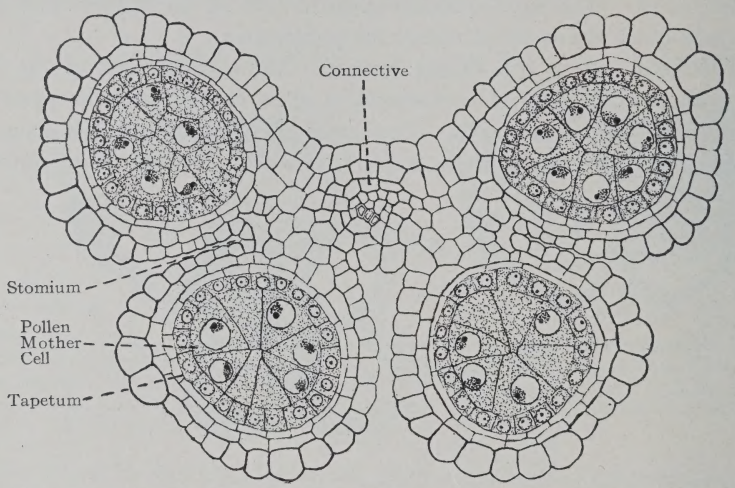


FIG. 439.—Cross section of anther of Johnson grass (*Holcus halepensis L.*).

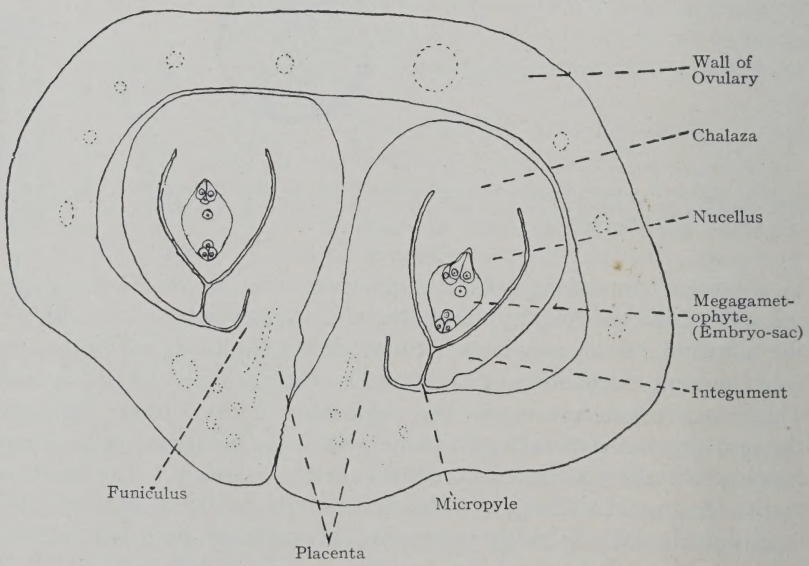


FIG. 440.—Cross section of the ovulary of the dwarf Larkspur (*Delphinium tricorne*), showing two ovules cut longitudinally.

idial cell divides before the pollen is shed. The wall of the pollen spore consists of two layers, the exine and intine. In some plants, as in Lilium, the exine is in the form of a beaded net which covers the intine with the

exception of an elliptical area known as the germ pore. The intine is a soft thin layer rich in pectine. The pollen spores spring from pollen mother-cells in the young anther. Their development will be described in a later paragraph.

The Ovule.—We may become familiar with the fully formed ovule (megasporangium) by noting the parts as seen in a longitudinal section. The plant selected as an illustration here is the Dwarf Larkspur (*Delphinium tricorne*), and a longitudinal section of the ovule with its attachment to the placenta is secured by taking cross sections of the simple pistil (Fig. 440); or the diagram of a longitudinal section of a pistil as shown in Fig. 446 may be consulted. The central and somewhat conical part of the ovule is the nucellus surrounded by the integument. Within the nucellus is the seven-celled megagametophyte. As in the pine ovule, the free end of the integument forms the micropyle. The integument and

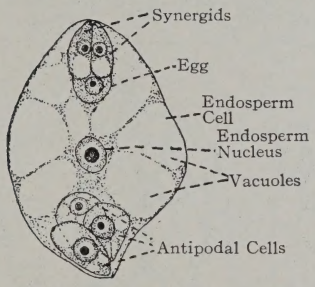


FIG. 441.—Embryo-sac of *Delphinium tricorne.*

nucellus which are united at the base are continued backwards into the stalk or funiculus connecting the ovule with the placenta. In some plants the funiculus is very short, in others it is distinguishable as a little cord. The nucellus and funiculus may form a straight line, or the ovule may be folded over as in the figure, so that funiculus and integument are united laterally, and the micropyle is brought near to the placenta. At the base of the nucellus is the chalaza.

The Megagametophyte, or Embryo-sac.—As stated above, the typical megagametophyte, more commonly referred to as the embryo-sac, consists of seven cells at the time of fecundation. The group of three cells in the micropylar end constitutes the egg-apparatus; the three at the chalazal end, the antipodal cells, and the large cell between containing one or more large vacuoles is the primary endosperm cell. It is very evident that the large endosperm cell makes up the bulk of the megagametophyte (Fig. 441). In the egg-apparatus, the cell which is usually inserted more deeply is the *egg*. It is pear-shaped, and may be recognized by the fact that the nucleus and cytoplasm lie in the lower and larger end, while the

upper end is occupied by a vacuole. In the other two cells of the egg apparatus, the *synergids*, the nuclei and cytoplasm lie in the upper ends of the cells and the vacuoles in the lower ends. In the Larkspur the three antipodal cells are much larger than those of the egg-apparatus and more densely filled with cytoplasm.

In the Angiosperms as a whole the antipodal cells represent a very variable group. In some plants these cells are not formed at all. In

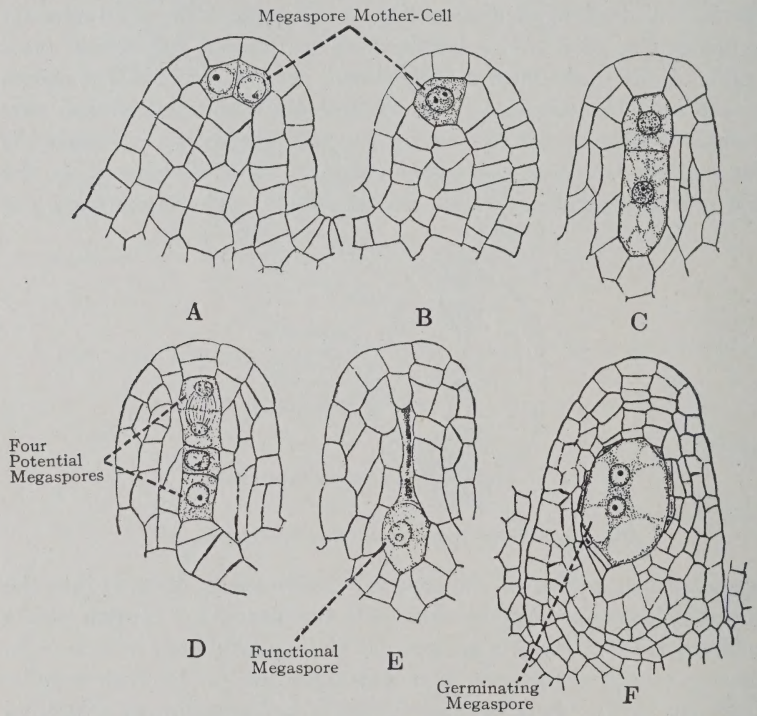


FIG. 442.—*Delphinium tricorne*. Longitudinal sections of several stages in the development of the ovule and megaspores, the nucellus only being shown. A, B, nucellus before the appearance of the integument, the megaspore mother-cells shown with contents. C, megaspore mother-cell has divided; D, the tetrad of four potential megaspores are present; E, the functional megaspore is germinating, and the three other megaspores above are being digested and absorbed; F, megaspore with two nuclei.

others, as in certain lilies, they may be poorly and incompletely developed, while in others they divide to form a larger mass of cells. In the latter case their role is probably that of elaborating food.

The Development of the Ovule, Megaspores, and Megagametophyte. This seven-celled megagametophyte and the ovule will doubtless be better understood if a few steps in the development of each are followed.

In the primordium of the ovule, the nucellus is the first to appear as a small protuberance upon the surface of the placenta (Fig. 442, A, B).

At the base of the nucellus the integument next appears as a fold growing up around and finally covering the nucellus. A conspicuous hypodermal cell (sometimes two in this plant) is now recognized at the apex of the nucellus. This is the megaspore mother-cell. With further growth, the megaspore mother-cell by two successive divisions gives rise to a tetrad of

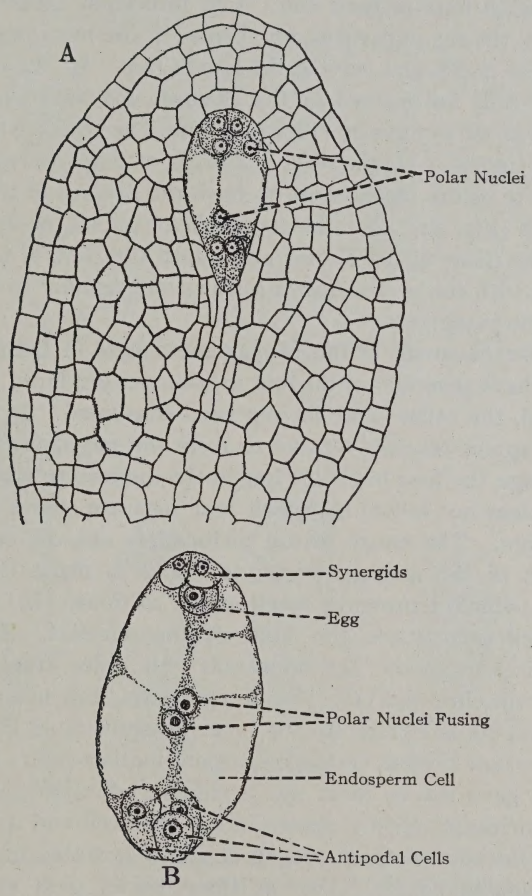


FIG. 443.—*Delphinium tricorne*. The concluding stages in the development of the ovule and megagametophyte. A, developed nucellus showing position of nearly mature megagametophyte. B, later stage; the polar nuclei are approaching each other.

four potential megaspores, arranged generally in an axial row (C, D). At this stage the integument (not shown in the figure) equals the height of the nucellus.

One of the potential megaspores, that nearer the chalaza, becomes functional, and, by further growth, enlarges and consumes the other three

potential megaspores, as well as the adjacent cells of the nucellus (E). This magaspore enlarges rapidly and its nucleus divides. One daughter nucleus passes to one end of the spore and the other to the other end. A large vacuole occupies the center (F). These nuclei soon divide and two nuclei are present in each end of the spore. These also divide, giving rise to four in each end. Cell formation takes place, by which three cells, the egg apparatus, are formed in the micropylar end involving three of the nuclei and leaving the fourth free. In like manner the three antipodal cells are formed in the chalazal end with the fourth nucleus lying free in the cytoplasm (Fig. 443, A). The two free nuclei are termed the polar nuclei. In the vast majority of angiosperms the two polar nuclei unite before fecundation to form the nucleus of the primary endosperm cell (Fig. 443, B). In a number of plants, as in some species of Lilium, the polar nuclei do not unite until the time of fecundation when they fuse with the second sperm nucleus in a manner to be described in a subsequent paragraph.

The Development of the Megagametophyte in Lilium.—In the foregoing we have seen that of the four megaspores produced, only one became functional, the other three having been consumed. In Lilium, however, the four spores *function together* to form the megagametophyte. In the tetrad stage the four nuclei lie free in the megaspore mother cell, i.e., cell division does not follow by which four separate spores are formed as in Delphinium. The entire tetrad included in one cell contributes to the formation of the megagametophyte. This is made clear in Fig. 444, A to F, which represents longitudinal sections. In A the megaspore mother-cell constitutes the bulk of the nucellus. The beginning of the inner integument has appeared. An older stage (B) shows the enlarged nucellus and the two integuments, the inner and the outer. The micropyle is formed by the inner integument in this species. Two nuclei are now present in the megaspore mother-cell. The nuclear division that gave rise to them was a reducing division. The result of the second nuclear division is shown in C. The cell and its four nuclei constitute a tetrad of megaspores, all of which as stated function in forming the megagametophyte. Two of these nuclei pass to the micropylar (upper) end of the cell and two to the opposite or chalazal end (D). All nuclei now divide, with the result that four occupy each end of the cell (E). Cell division follows, and three cells are organized in the micropylar end to form the egg apparatus, three in the chalazal end which are the antipodal cells, while the two polar nuclei remain free in the large central cell, the primary endosperm cell. As in the Larkspur the egg apparatus consists of the egg and two synergids. In *Lilium martagon* and *L. candidum*, the three antipodal cells are not always normally developed, and

the group may soon disorganize. The polar nuclei approach but do not fuse until the arrival of the second sperm nucleus (Fig. 447).

In typical Angiosperms, the megagametophyte consists of the *seven-celled* structure as described in the foregoing. There are many exceptions. In some cases this structure may possess fewer cells than seven, as the

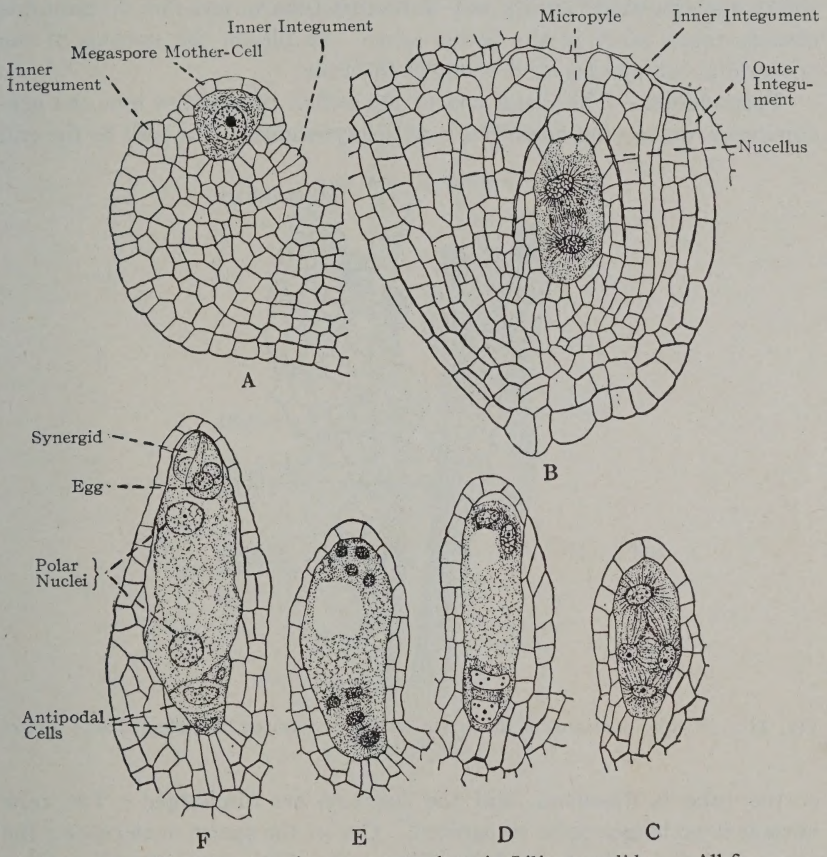


FIG. 444.—Development of megagametophyte in *Lilium candidum*. All figures are longitudinal sections. A, young ovule; the megaspore mother-cell comprises the bulk of the nucellus. B, older stage of ovule; the nucleus of the megaspore mother-cell has divided. C, megaspore mother-cell with four tetrad nuclei. D, two nuclei in each end of the cell. E, four nuclei in each end. F, megagametophyte ready for fecundation.

antipodal cells may not be formed at all; in still other cases the antipodal cells may divide giving rise to a more massive tissue.

The Microgametophyte.—A functional pollen spore having reached the stigma, the tube cell begins growth and develops a slender tube which makes its way through the stigma and style into the ovulary, and

continues until its distal end reaches the egg apparatus (Figs. 445, 446). The tube nucleus and antheridial cell together with all the cytoplasmic contents of the pollen grain pass down into the end of the tube (Fig. 446, B). The tube nucleus is always near the end of the tube and presides over its growth. The nucleus of the antheridial cell (generative cell) divides into the two sperm nuclei on its way down the tube unless this division has already taken place in the pollen spore. In Lilium the nucleus of the antheridial cell divides after it enters the tube.

Fecundation.—The distal end of the pollen tube grows into the egg-apparatus, destroying one or both of the synergids. The wall at the end

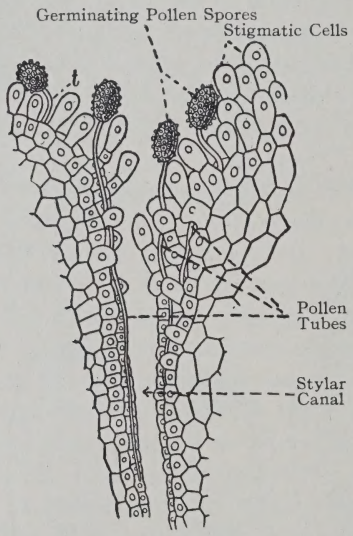


FIG. 445.—Portion of stigma of the lily in section penetrated by pollen tubes. (After Dodel-Port.)

of the tube is dissolved, and the contents are discharged. The tube nucleus is no longer to be recognized. One of the sperm nuclei enters the egg and fuses with its nucleus (Fig. 447). The other sperm nucleus is usually absorbed as food. In some plants the second sperm nucleus unites with the two polar nuclei to form the nucleus of the endosperm cell. This occurs in some species of Lilium and in a number of other plants. As stated in a preceding paragraph the polar nuclei in such cases do not fuse until the second sperm nucleus arrives. The fusion of the two polar nuclei and second sperm nucleus is sometimes referred to as a second fertilization, and the fusion of the two sperms with egg and polar nuclei respectively, double fertilization. The process is illustrated in Fig. 447, A, B.

The fusion of the second sperm with the polar nuclei is without significance save in a few plants. The most notable of such plants is Indian corn, *Zea mays*, in which this fusion is now acknowledged to be responsible for the phenomenon known as *xenia*, or the effect of the pollen upon the endosperm. More definitely stated xenia consists in imparting the dominant endosperm characteristics of the pollen parent to the endo-

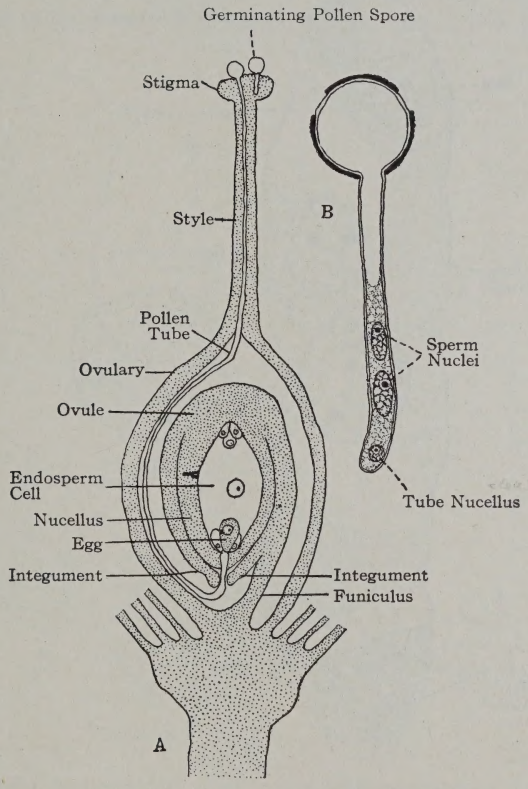


FIG. 446.—A, diagram of a longitudinal section of a pistil with one ovule. B, pollen spore which has developed a pollen tube.

sperm of the seed of the ovulate parent. To illustrate, if the ovulate flowers of a sweet corn plant whose endosperm would be normally sugary, if pollinized from a sweet corn parent, be pollinized with pollen of field corn whose endosperm is starchy, the result will not be sugar corn but starchy corn. Starch will prevail in the endosperm instead of sugar, the starchy characteristic being transmitted presumably by the second sperm nucleus which probably unites with the polar nuclei.

In Lilium the union of the second sperm nucleus with the polar nuclei produces no visible effect upon the endosperm.

During the development of the seed the nucellus is usually consumed. As the seed matures, the integument or integuments die and become the dead and dried seed coat.

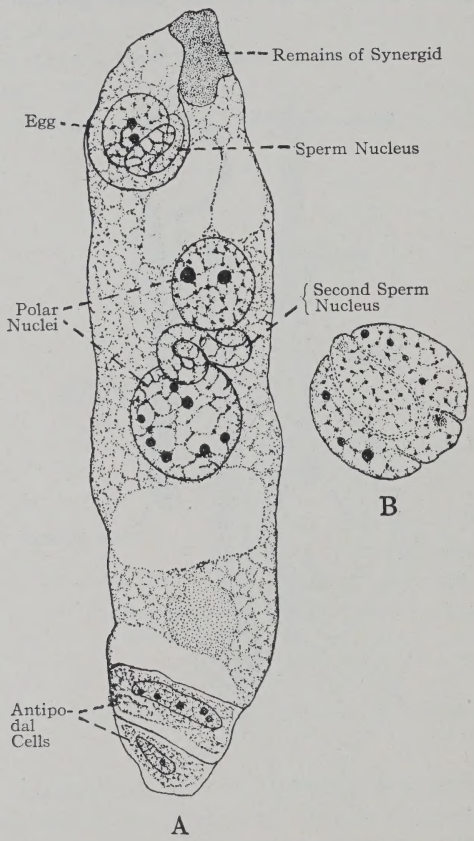


FIG. 447.—*Lilium martagon.* A, megagametophyte at the time of fecundation; sperm nucleus uniting with nucleus of the egg; second sperm nucleus uniting with polar nuclei. B, the fusion of second sperm nucleus and polar nuclei almost complete.

The dandelion and certain other plants belonging to the Compositae produce seeds without the function of pollen. The phenomenon is known as *apogamy*.

The Development of the Dicotyledonous Embryo.—Following fecundation two structures begin development from the megagametophyte, namely, the embryo from the zygote, or fecundated egg, and the endosperm from the primary endosperm cell.

To illustrate very briefly the development of the embryo, a few steps in the process will be presented from that of Capsella (Bursa) which is shown in Fig. 448.

The zygote elongates and divides transversely into a short row of cells, the proembryo (A). The terminal, or distal, cell of this row, that farthest from the micropyle, becomes the body of the embryo (*e*) while the others give rise to the suspensor (*s*). In the stage (A) the terminal cell is divided lengthwise. The suspensor becomes a row of about eight

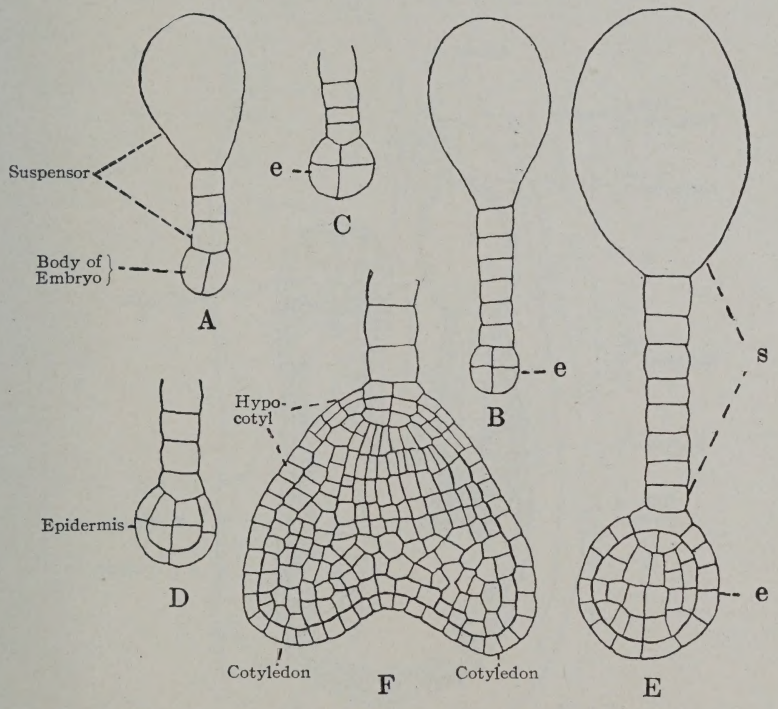


FIG. 448.—*Capsella bursa-pastoris*. Embryos in different stages of development dissected out of the ovules; *s*, suspensor; *e*, body of embryo.

or ten cells. The cell nearest the micropyle (A, B, E) is greatly enlarged. By the elongation of the suspensor the body of the embryo is pushed down into the endosperm cavity. The body of the embryo enlarges, becoming globular, and by transverse and longitudinal cell divisions there result two tiers of four cells each (B, C). The terminal tier of four cells will give rise to the cotyledons and apex of the stem, the basal tier will form the hypocotyl, and from the basal end of the hypocotyl will ultimately develop the root.

The two tiers of four cells each mentioned above divide parallel with the outer surface of the embryo, cutting off the layer of primary epidermal cells (D).

The body of the embryo remains globular for a time (E). Very soon, however, the distal end becomes broad and somewhat flattened. Here growth is localized at two opposite points which is manifested in the appearance of two protuberances or lobes of equal size (F). These are

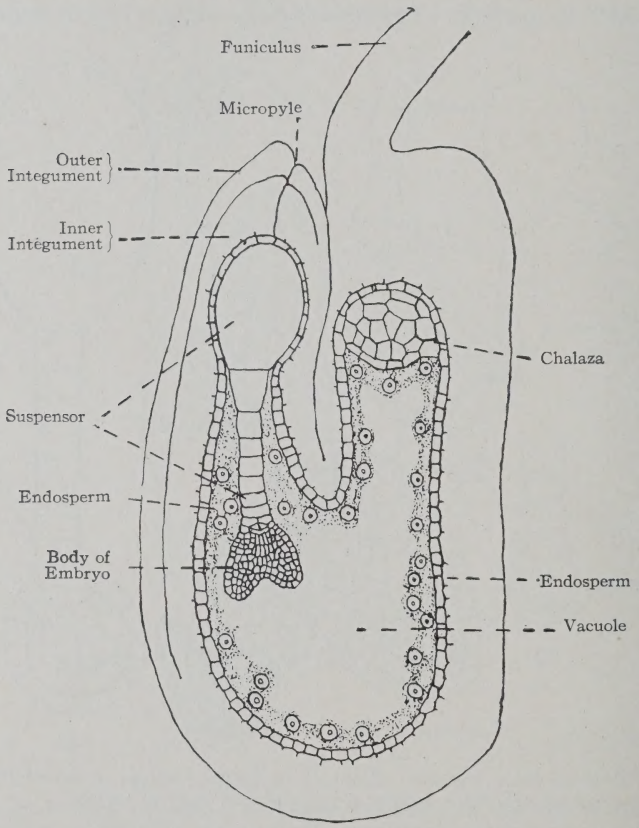


FIG. 449.—Capsella. Longitudinal section of an immature seed containing embryo and a wall layer of endosperm. (Adapted from Bergen and Davis' "Principles of Botany." By permission of Ginn & Company, Publishers.)

the primordia of the two cotyledons. Between the two cotyledons the epicotyl will develop later. Fig. 449 is a section of a young seed with small embryo in position. In Capsella the embryo grows rapidly consuming the endosperm almost as rapidly as it is formed. When the seed is mature a large embryo differentiated into a hypocotyl and two large cotyledons fills the cavity of the seed, no endosperm being present.

The Embryo of a Monocotyledonous Plant.—As an illustration a few earlier stages in the embryo development of Sagittaria will be selected. As in the case of a dicotyledonous embryo the zygote gives rise first to a proembryo consisting of a row of cells, as shown in Fig. 450, A. The terminal cell (*c*) will give rise to the cotyledon; the middle cell (*b*) to the hypocotyl,

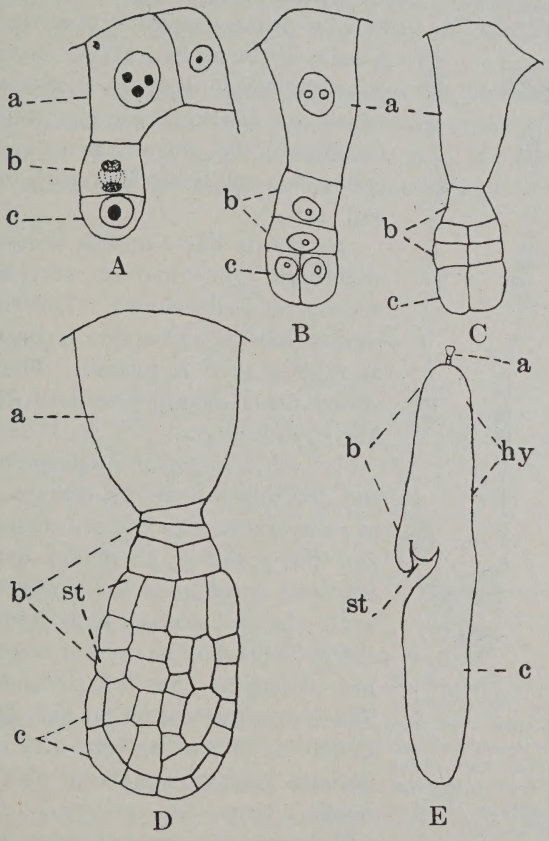


FIG. 450.—Sagittaria. Longitudinal sections of embryos in different stages of development. A, embryo, a row of three cells, *a*, *b*, *c*, and a remaining synergid. B, C, D, older stages. E, nearly mature embryo; *st*, stem apex. (A–D adapted from Schaffner.)

stem tip, and some suspensor cells, while the basal cell (*a*) is the large part of the suspensor. B, C, and D are successively older stages. The parts that have developed from cells *b* and *c* are indicated respectively by these letters in D. Fig. E is an outline (diagrammatic) of a longitudinal section of the nearly mature embryo. It is clear that the entire distal end of the embryo becomes the cotyledon. The tip of the stem (*st*) is seen in

a depression at one side. The stem tip is partly surrounded by the base of the cotyledon.

The Development of the Megagametophyte (Endosperm) Following Fecundation.—The growth of the endosperm from the large primary endosperm cell begins simultaneously with the development of the embryo. In typical cases the ovule gradually enlarges, and the primary endosperm cell increases enormously in size by hydration. By repeated nuclear divisions, there arise many free nuclei which are distributed in the parietal layer of cytoplasm, the central cavity of the primary endosperm cell being filled with cell sap (Figs. 449, 451).

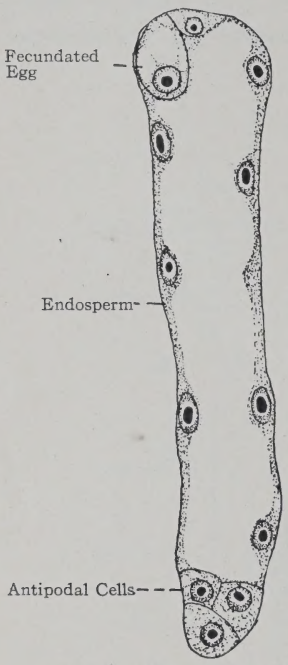


FIG. 451.—A longitudinal section of the megagametophyte a short time after fecundation. The fecundated egg has not divided; the endosperm consists of a parietal layer of cytoplasm with a number of free nuclei.

In plants like Capsella whose seeds lack endosperm when mature, very little cellular endosperm is developed. The embryo grows so fast that the endosperm is consumed almost as rapidly as it is formed. The result is, as stated above, a mature seed with a large embryo but no endosperm.

In other types of Angiosperms, however, the development of the embryo is less rapid in comparison with the growth of endosperm, and the result is a smaller embryo and a relatively large mass of endosperm (Figs. 452, 453). In such plants a large number of endosperm nuclei may be present before the zygote has undergone the first division (Fig. 451). The megagametophyte at this stage consists, therefore, of the antipodal cells and the parietal layer of cytoplasm with a number of nuclei. Near the embryo, cell formation will begin and proceed along the periphery of the primary endosperm cavity and towards its center until the entire space is filled. Fig. 452 illustrates the micropylar end of a nearly mature seed in one of the Ranunculaceae (*Actaea alba*) as seen in longitudinal section. The relatively small embryo is completely surrounded by the cellular endosperm. Fig. 453 is in an outline of a section of a mature seed of the same plant.

The Maturing of the Seed and the Formation of the Fruit.—During the development of embryo and endosperm, changes take place in the nucellus and integuments of the ovule. In the type represented by Capsella, the nucellus is consumed at an early stage, and the integuments

are changed into the seed coat, whose dead cells are crushed and flattened into the two thin layers. In some Angiosperms the large nucellus of the ovule is not consumed during seed development, but it persists and remains in the mature seed where it is known as *perisperm.* In the meanwhile, as the ovules grow and mature into seeds, the pistil enlarges also through growth and becomes transformed into the fruit. The small ovulary of the tulip, for example, becomes the large capsule of the mature fruit (Fig. 433, C).

The Difference between Seed Formation in Gymnosperms and Angiosperms.—When we recall the process of seed formation in Gymnosperms, it is seen that the bulk of the endosperm is developed before fecundation, whereas in the Angiosperms the endosperm is formed after

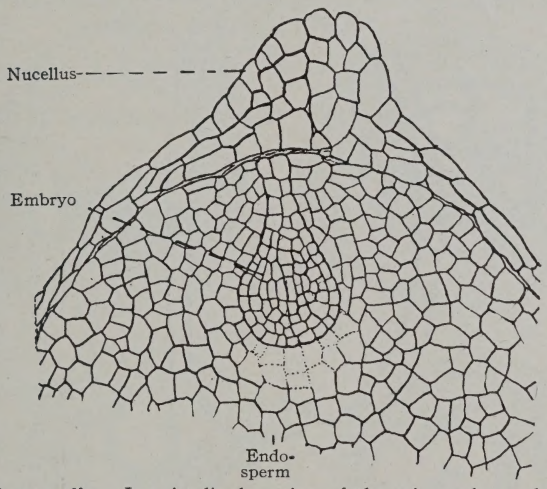


FIG. 452.—*Actaea alba.* Longitudinal section of the micropylar end of an immature seed, the integument being omitted.

fertilization. In all Gymnosperms with the exception of Gnetum, an archegonium, an organ characteristic of Bryophyta and Pteridophyta, is present, while in Angiosperms the archegonium is probably represented by the egg alone.

The Development of the Pollen from the Pollen Mother-cells.—In all groups of plants from Bryophyta to Spermatophyta, and in such Thallophyta as Dictyota of the Brown Algae and Polysiphonia of the Red Algae, it was pointed out (1) that certain spores developed by the diploid structure, were produced in groups of four, *tetrads,* from mother-cells designated as *spore mother-cells,* and (2) that the first nuclear division leading to the formation of the tetrad was a reducing division, by which it is meant that the number of chromosomes characteristic of the diploid

structure was reduced to one-half. As a result of the reducing division, the spores and the gametophytes developed from them possess the haploid number of chromosomes. Probably in no other cells in the plant kingdom may the reducing nuclear division be so clearly and definitely followed in all details as in the pollen mother-cells of certain species of Lilium. The following description pertains especially to *Lilium candidum* and *Lilium martagon*.

The Heterotypic Mitosis, or Reducing Division.—After the somatic, or equational, nuclear divisions have been completed in the sporogenous tissue of the anther, the pollen mother-cells, which are polyhedral in shape, make up a compact tissue without intercellular spaces. The cell walls

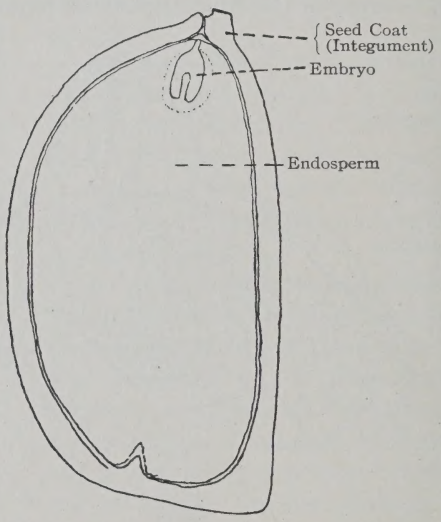


FIG. 453.—*Actaea alba*. Outline of a longitudinal section of a mature seed.

are thin, the cytoplasm dense and rather uniform in structure, and the nuclei are relatively large.

The Resting Stage.—In the nucleus the numerous small and irregular chromatin granules varying in size are held upon a delicate linin network. The linin threads are seen connecting the chromatin granules or masses. One to several nucleoli may be present (Fig. 454, A). When the chromatin is in the finely divided state as just stated, the nucleus is said to be in the resting stage. The beginning of mitosis is indicated by an increase in size of the cell and of the nucleus.

The First Contraction.—The next conspicuous change that takes place is seen in the contraction, or balling up, of the nuclear contents into a dense mass at one side of the nuclear cavity (B). The nucleolus is usually included in the contracted mass. This stage persists for some

time, during which the nucleus has increased further in size, and the cell contents tend to round off at the corners.

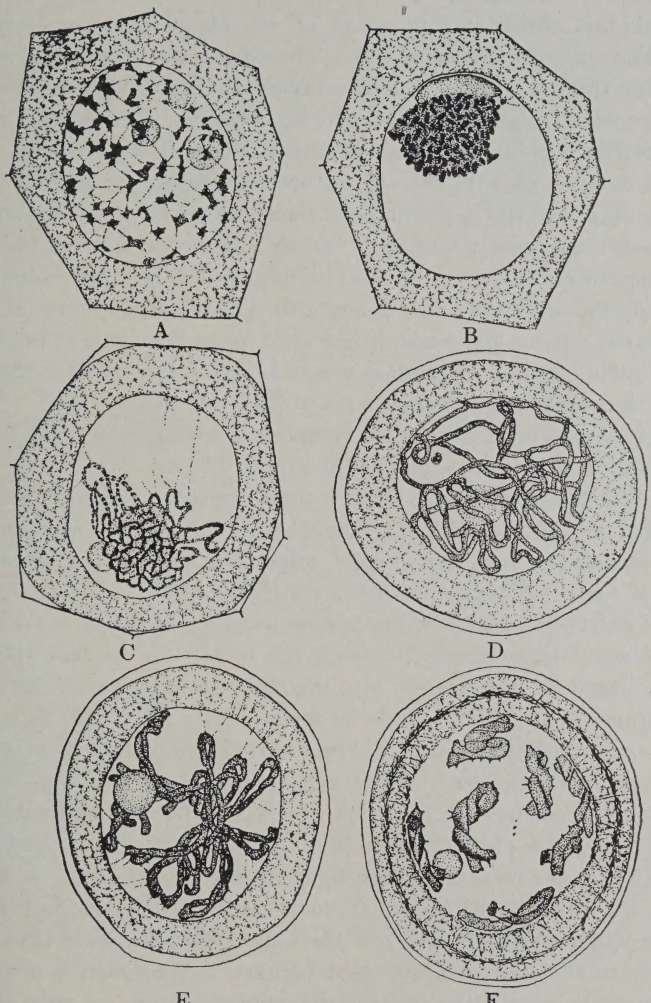


FIG. 454.—Development of the pollen from the pollen mother-cell in Lilium. A, the nucleus is in the resting stage; B, the first contraction; C, loosening up of the contracted mass. D, the hollow spirem; E, second contraction, loops radiating from a central tangle; F, cross segmentation of spirem completed and bivalent chromosomes (pairs) have been formed.

The Formation of the Spirem.—Following the period of the first contraction, the contracted mass begins to loosen and spread out in the nuclear cavity, when it is seen that a continuous chromatin thread, spirem, has

been formed (C). The loops and turns of the thread or spirem spread farther and farther apart, and soon become somewhat evenly distributed in the nuclear cavity (D). A very careful study reveals the fact that this thread is composed of chromatin discs or very small masses known as *chromomeres* (C). The chromomeres are held together in the linin thread. Under the most favorable circumstances the chromomeres are seen to be divided lengthwise, and this phenomenon is interpreted as the beginning of a longitudinal fission of the spirem.

With further growth, the spirem becomes thicker and more uniform in appearance, and the individual chromomeres are no longer recognizable. At this stage the longitudinal split can also be seen at least in places, but as the spirem continues to thicken its double nature may be completely concealed, and we have what is now called the hollow spirem (D). The spirem is continuous and without free ends in the species here in question. As the diploid number of chromosomes in Lilium is twenty-four, the spirem represents twenty-four chromosomes united end to end.

In the meantime the cell has completely rounded off, and has built about itself a new wall, which is thick and soft.

The Second Contraction.—During the next stage the spirem becomes rearranged in part, by which a tangle or knot is formed near the center of the nucleus. From this tangle other portions of the spirem may radiate as loops. This is the second contraction (E).

The Cross Segmentation of the Spirem and the Formation of the Bivalent Chromosomes.—Immediately following the second contraction, the spirem begins to segment transversely into the chromosomes, and these chromosomes approximate side by side to form pairs. Each pair is a *bivalent chromosome*, consisting of two distinct chromosomes that were arranged end to end in the spirem. There are, therefore, twelve pairs or twelve bivalent chromosomes in Lilium. In the state of the second contraction, some of the loops of the spirem that radiate from the tangled portion represent two chromosomes that tend to remain attached for a longer time at the bend of the loop. In such cases the bivalent is formed by the approximation of the sides of the loop. The bivalents thus formed are likely to resemble a figure eight because of the twisting of the loop.

After cross segmentation and the approximation in pairs to form bivalents, the bivalents move apart and become more regularly spaced within the nuclear cavity (F). In this figure, eight of the twelve bivalents are shown.

The bivalents may present different forms, depending upon whether the two members are straight or bent, and upon the manner in which they lie with reference to each other. In most cases the two members of the bivalent lie in close contact side by side, but they are almost always

twisted about each other. If the members diverge at one end, a Y-shaped bivalent is seen; if both ends diverge, an X-shaped figure results. A

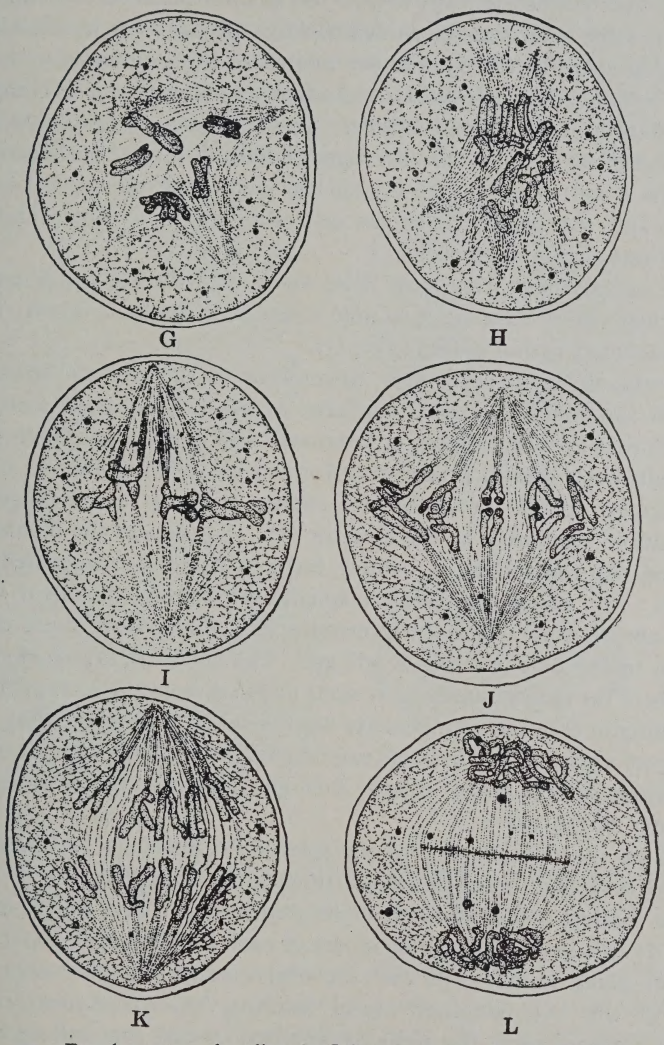


FIG. 455.—Development of pollen in Lilium continued. G, H, the multipolar spindle. I, mature spindle. J, members of the bivalent chromosomes separating; each member has split lengthwise, and the two halves diverge at their equatorial ends. K, anaphase; L, telophase, the chromatin is forming the daughter nuclei.

loop or a circle is formed when the two members bend apart at the middle and remain in contact at the ends. Some of the bivalents are bent in the form of a U. Those that are bent and twisted most are those that

were formed from the knotted or tangled part of the spirem in the second contraction stage. In every case, no matter what form the bivalent may present, each consists always of two rod-shaped chromosomes that have paired in some such manner as described. All the steps in mitosis from the resting stage to the spindle are known as the prophases.

The Spindle Stage, Metaphase.—As soon as segmentation is completed, the formation of the spindle begins. The spindle fibers originate wholly in the cytoplasm. They are arranged radially from the nucleus, or they may form a weft parallel with the nuclear membrane midway between the nucleus and the periphery of the cell (Fig. 454, F). Sometimes both orientations of the fibers occur.

The nuclear membrane now fades away, and the spindle fibers enter the nuclear cavity forming a spindle complex with the bivalent chromosomes included within it (Fig. 455, G).

Certain of the fibers attach themselves to the chromosomes. The fibers of the spindle complex converge at several points to form poles, in which case the whole figure is designated as a *muti-polar spindle* (G, H). The multi-polar spindle is soon transformed into the regular and symmetrical bipolar spindle in which the twelve bivalents are arranged with considerable regularity at the equator (I). Sometimes the bivalents are arranged like the spokes of a wheel, but as a rule the arrangement is less regular. Fig. 455, I, represents a spindle in which four bivalent chromosomes are shown. From each member of a bivalent a sheaf of fibers extends to the pole to which it will go. The fibers are attached either to the ends of the chromosomes or at some distance from the ends at the place of bending in case the members are bent or when they form a ring, a loop, or a figure eight. Certain fibers extend from pole to pole without touching the chromosomes, while others diverge from the poles towards the periphery of the cell.

During the development of the spindle the nucleolus becomes broken up, and very small nucleoli are scattered in the cytoplasm.

The Passage of the Members of the Bivalents to Their Respective Poles, or the Anaphases.—The two members of each bivalent now separate, one member going to one pole and the other member to the other (J, K). Each of the two daughter nuclei resulting will consequently possess twelve chromosomes, the reduced number, or just one-half as many as were present in the mother-cell.

On their way to the poles the members of the bivalents undergo a change such as takes place in no other nuclear division. As the members separate and sometimes before they separate in metakinesis, each is seen to be split longitudinally (J). This is the longitudinal fission that was observed in the spirem of the prophases. This fission is a preparation for

the second mitosis, i.e., the one that is soon to follow. The two segments resulting from the longitudinal fission pass to the pole side by side, the ends nearest the pole being attached to the sheaf of fibers, while the two ends nearest the equator may diverge to produce the V-shaped figure. If the two members of the bivalent were not attached to the spindle fibers at the ends, but at some distance from the ends, as in the ring-shaped bivalent or that like a figure eight, then the two segments resulting from the longitudinal split would present the form of two U's in contact side by side.

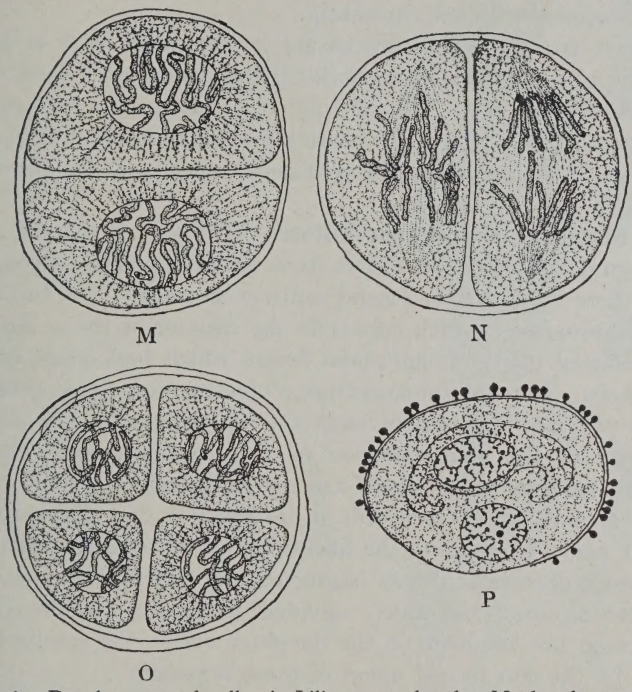


FIG. 456.—Development of pollen in Lilium completed. M, daughter cells resulting from the first division. N, a step in the second division. O, tetrad of four pollen spores. P, mature pollen spore; the crescentic antheridial cell lies free inside the tube cell.

The Construction of the Daughter Nuclei, the Telophases.—When the chromosomes reach the poles, they are, as a rule, closely crowded or massed. The cytoplasm soon seems to withdraw from the mass of chromosomes leaving a colorless cavity at whose periphery a nuclear membrane is formed. The spindle fibers connecting the two daughter nuclei are now called *connecting fibers*.

The behavior of the chromatin during the construction of the daughter nuclei depends upon the lapse of time between the first and second mitoses.

If the second division follows the first immediately, as happens in Lilium during warm weather, the chromosomes on arriving at the poles will all join end to end to form a spirem at once, and the second division will begin without an intervening resting stage (L, M). But, if some time intervenes between the two mitoses, the chromosomes will fragment or recticulate into smaller pieces, so that all identity of the former segments is lost. This reticulation may even proceed to the extent of forming a resting stage. A nucleolus appears in each daughter nucleus, usually closely associated with the chromatin.

As soon as the daughter nuclei are formed, a *cell plate* is developed across the cell at the equator, dividing the pollen mother-cell into two daughter cells (L, M). The cell plate is a plasma membrane, formed by the connecting fibers. This plasma membrane splits into two to provide plasma membranes for the contiguous surfaces of the two daughter cells.

The Second or Homeotypic Mitosis.—The second mitosis, i.e., that of the two daughter nuclei, differs from the first, or heterotypic mitosis, in that there is no first or second contraction stage. The two segments of each chromosome which appear in the equator of the second mitosis were produced by the longitudinal fission which took place during the first mitosis. They do not constitute a bivalent, for, as has been pointed out, the two members of a bivalent are not the result of a longitudinal fission but of the approximation of two chromosomes. The second mitosis is therefore an *equational* and not a reducing division.

The second mitosis proceeds as follows: if the chromatin of the daughter nuclei passed into the finely divided state of the resting stage, or became broken into coarser fragments, the spirem is formed from the fragments or from the finely divided chromatin; if the chromatin segments do not fragment in the daughter nuclei, the spirem is formed directly by the end to end union of those segments.

The spindle is formed as in the first mitosis, i.e., from a multipolar complex of fibers derived from the cytoplasm.

The spirem segments crosswise presumably into the identical segments that came to the daughter nucleus. These segments are arranged upon the spindle in pairs, being attached end to end or side by side (Fig. 456, N). The two members of each pair are supposed to have been derived from one and the same chromosome by the longitudinal division observed in the preceding anaphases. There is no means of knowing, however, that this is so.

In the equator the segments are usually massed together or much entangled. They may radiate from the spindle or lie tangentially upon it (N, left).

With the beginning of the anaphases, the segments (grand daughter chromosomes) separate and pass to the poles (N, right). The granddaughter nuclei are organized, and cell division takes place as in the first mitosis (O).

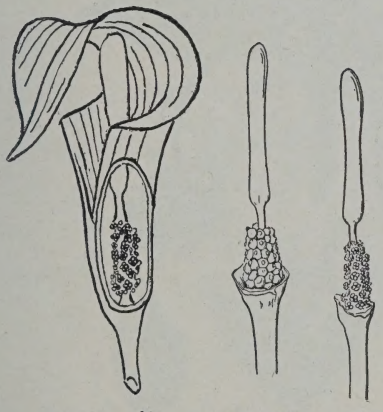


FIG. 457.—Inflorescence of Indian turnip (*Arisaema triphyllum*). A, spadix surrounded by the overarching spathe which is partly cut away at the side to expose the staminate flowers. B, spadix with pistillate flowers. C, one with staminate flowers.

FIG. 458.—Flowers and fruit of willow (*Salix viminalis*). A, twig with staminate catkins. B, staminate flower with subtending bract, enlarged. C, pistillate catkin. D, E, pistillate flowers, enlarged. F, fruit natural size. G, the same enlarged. H, seed enlarged. (Strasburger, Macmillan Co.)

Maturing of the Pollen.—We now have a tetrad of four pollen spores, each of which matures into a pollen grain of two cells. By the dissolution of the wall of the mother-cell the spores are set free in the cavity of the anther, and each rounds out, becoming globular or elongated. A wall of two layers is developed, the exine and the intine. The spore divides

in such a manner that one of the cells is crescentic in shape and lies inside the other (P). This crescentic cell, the *antheridial* cell (generative cell), is provided only with a plasma membrane. The cell provided with the double wall of intine and exine is called the tube cell, as pointed out in a preceding paragraph.

Kinds of Flowers

Staminate and Pistillate, or Diclinous Flowers.—As stated above, a flower consists of one or more spore-bearing members with or without

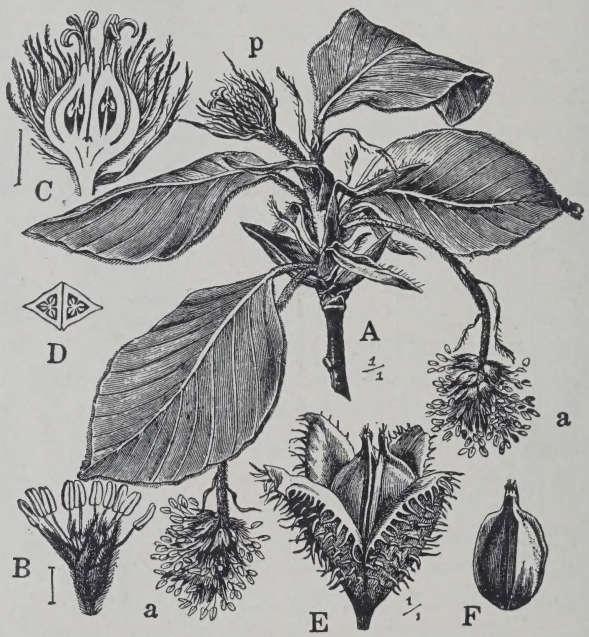


Fig. 459.—Flowers and fruit of beech (*Fagus sylvatica*). A, twig with staminate, *a*, and pistillate, *p*, flowers. B, staminate flower. C, pistillate flower halved lengthwise. D, cross section of ovulary. E, fruit with husk open. F, one of the triangular nuts. (After Wossidlo.)

accessory parts. A single stamen or a single pistil may constitute a flower. Flowers which consist of one or more functional stamens only, are staminate flowers, and those composed of one or more pistils only, are pistillate flowers. Staminate flowers and pistillate flowers borne separately are known as *diclinous* flowers, while those consisting of stamens and pistils are *monoclinous*. Diclinous flowers are characteristic of many of our forest trees (Figs. 458 to 464). The simplest kind of diclinous flowers are well illustrated in the jack-in-the-pulpit (Fig. 457) in which the pistillate flowers are single pistils, and the staminate

flowers consist each of one or two stamens. Diclinous flowers may be subtended by a bract as in the willows (Fig. 458) or surrounded by two or more bracts which make up an involucre as in the beech, hazel nut, and oak (Figs. 459, 460, 461). Some diclinous flowers may have one or both sets of perigone leaves.

In some plants the staminate flowers contain a rudimentary pistil, and the pistillate flowers rudimentary stamens. Such conditions have been

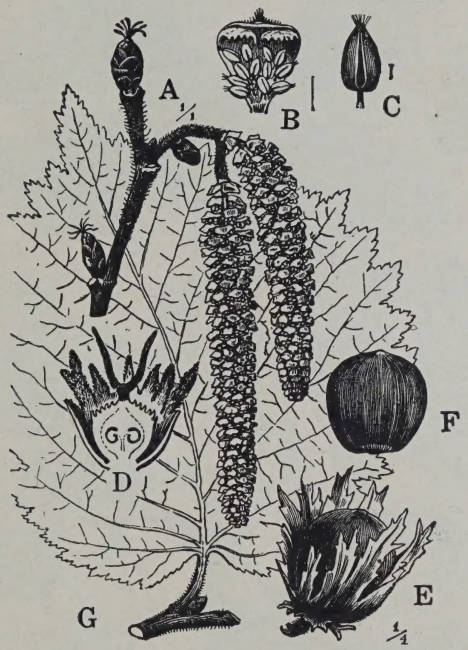


FIG. 460.—Flower and fruit of hazel nut (*Corylus avellana*). A, twig with flowers. B, staminate flower. C, stamen. D, pistillate flower in longitudinal section. E, fruit surrounded by involucre. F, nut with involucre removed. G, leaf. (After Wossidlo.)

brought about by the abortion of one or the other set of spore-bearing members.

Monoecism and Dioecism.—When diclinous flowers are borne upon the same individual, the plant is monoecious. Indian corn is typically monoecious, the staminate flowers constituting the tassel and the pistillate flowers making up the ear. When the diclinous flowers are borne upon different individuals, the plants are *dioecious*, as in the box elder (*Acer negundo*), the willows, and the willow-poplars (Populus). The expression, *complete* flower, is applied to those monoclinous flowers having calyx and corolla.

The Progressive Development in the Form and Structure of Flowers.—The typical monoclinous flower of our illustration, the tulip, has its parts arranged in circles or whorls of a definite number of parts. Such flowers are cyclic. Flowers in certain plants, however, consist of an indefinite number of parts which, like the carpels in a pine cone, are arranged

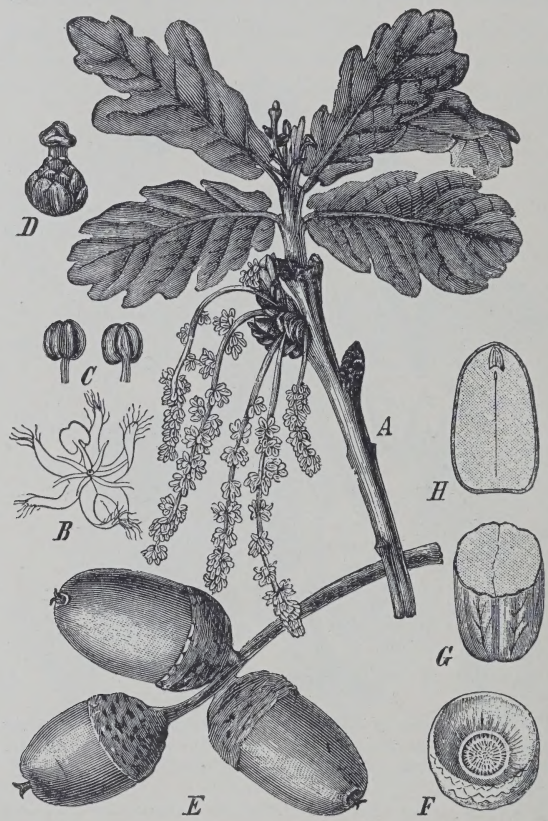


FIG. 461.—Flowers and fruit of the oak (*Quercus pedunculata*). A, twig with flowers. B, staminate flower. C, two stamens, D, pistillate flower, enlarged. E, fruit, acorns. F, cup with acorn removed. G, H, seed in longitudinal and cross section. The perianth of the staminate flowers consists of 5–7 segments; stamens 6–12. (After Wossidlo.)

spirally. The white water lily (*Castalia odorata*) is a good illustration. In this plant the parts of the flower are indefinite in number and spirally arranged. The petals tend to merge into stamens, i.e., some parts of the perigone are partly stamen (Fig. 466, A, B). The spiral arrangement is regarded as a more primitive type than that in which the smaller and definite number of parts are arranged in cycles, as is the case in most of

the flowering plants. There are good reasons also for believing that plants having flowers with perianths were evolved from plants whose flowers were without perianths, i.e., naked flowers are more primitive in character than those with perianths.

With the progressive development of the flower in angiosperms, which culminates in the orchid family of the monocotyls and in the Compositae

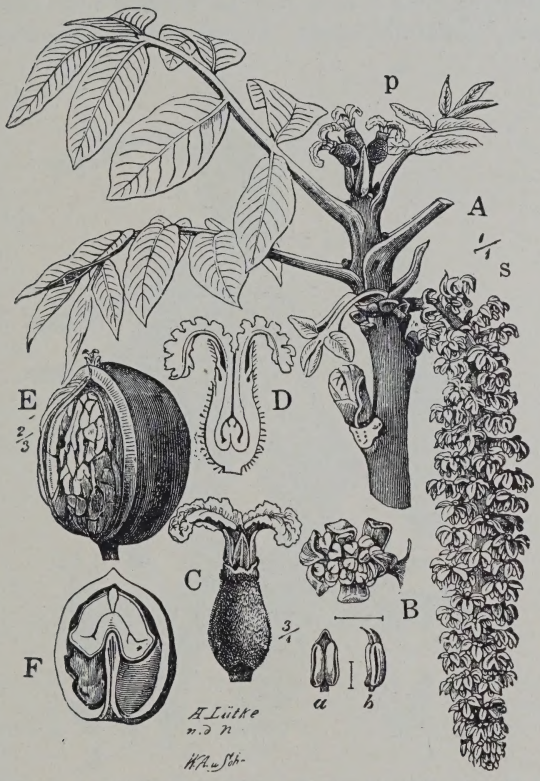


FIG. 462.—Flowers and fruit of the walnut (*Juglans regia*). A, branch with flowers; *p*, pistillate flowers; *s*, catkin of staminate flowers. B, staminate flower; *a*, stamen seen from inside; *b*, in profile. C, pistillate flower. D, the same in longitudinal section. E, fruit with one-half of husk removed. F, the nut halved lengthwise. (After Wossidlo.)

(dandelion and Aster) of the dicotyls, there have taken place certain definite changes. These changes pertain, first to the union of the parts of each circle, then to the union of the different circles into a more united structure.

Polypetalous and Sympetalous Flowers.—Petals and sepals are either separate or more or less united. Some flowers have united sepals and separated petals. Those with petals all separate, i.e., distinct as to their

attachment to the receptacle, are *polypetalous* (*choripetalous*). Examples are the garden tulip and peony (Fig. 467). If the petals are united into one piece, the corolla is gamapetalous (*sympetalous*). Phlox, morning glory, petunia, and jimson weed are examples.

Regular and Irregular Corollas.—When all the petals are of the same shape and size the corolla is *regular*. Such corollas are radially symmetrical (actinomorphic); they can be divided into two symmetrical halves in many radial directions. Corollas in which one or more petals

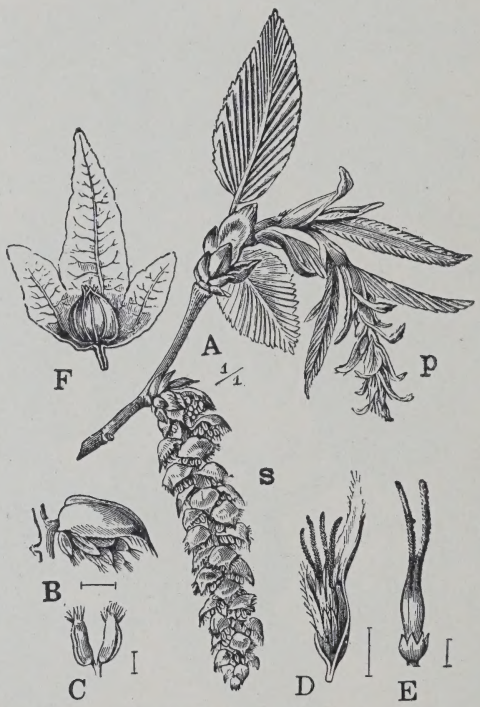


FIG. 463.—Flowers and fruit of water beech (*Carpinus betulus*). A, branch with staminate, *s*, and pistillate catkins, *p*. B, staminate flower. C, two stamens. D, pistillate flowers. E, a single pistillate flower. F, fruit with bract. (After Wossidlo.)

differ in shape or size from the others, are *irregular* (*zygomorphic*). They can be divided into two symmetrical halves in one plane only. The sweet pea, red clover, and snapdragon have irregular corollas.

Variation in the Androecium.—As a rule stamens are alike and attached to the receptacle as are other parts of the flower. In some cases, however, they are developed in two sets. In the sweet pea, red clover and some other members of the Leguminosae, one of the ten stamens is free, the other nine have their filaments united into one piece. In flowers with

sympetalous corollas the stamens are attached to the corolla. In one great group of plants to which the mallow, the cotton plant, and the hollyhock belong, the stamens form a stout column or tube enclosing the style (Fig. 468).

Variations in the Gynoecium.—As stated in a preceding paragraph, the parts of the gynoecium of the simpler types of flowers are borne separately upon the receptacle, the peony, buttercup and the marsh marigold (Caltha) being examples (Fig. 467). The pistils in such flowers

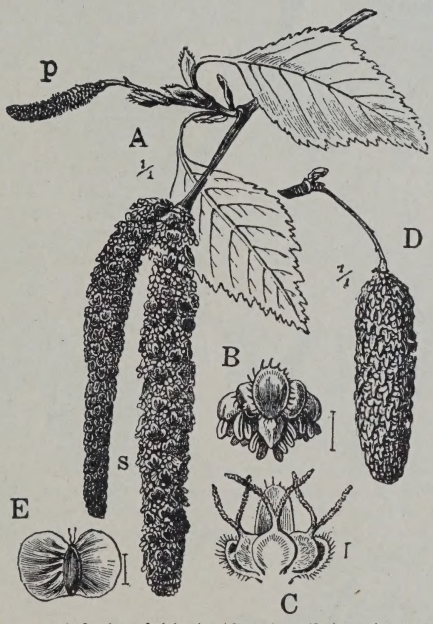


FIG. 464.—Flowers and fruit of birch (*Betula alba*). A, twig with staminate, *s*, and pistillate, *p*, catkins. B, three-lobed bract with three staminate flowers each having one scale. C, bract with three pistillate flowers. D, catkin of fruit. E, one fruit. (After Wossidlo.)

are simple, i.e., composed of one carpel. With the progressive change toward the higher types, there took place the union of the carpels into one piece and also a reduction in the number of parts. In the tulip, for example, the three carpels forming the compound pistil are united from an early stage in development.

Hypogynous, Perigynous, and Epigynous Flowers.—When all the parts are attached directly to the receptacle, the stamens and perigone below the base of the pistil or pistils, the flower is *hypogynous* (Figs. 467, 469, 1). In case the axis grows up to form a cup upon whose rim or margin the sepals, petals, and stamens are borne, but which does not unite with the pistil or pistils, the flower is *perigynous* (Fig. 469, 2). An *epigynous*

flower is one in which the axis and pistil are grown together so that stamens and perigone appear to arise from the top of the ovulary, as in the common apple (Fig. 469, 3).

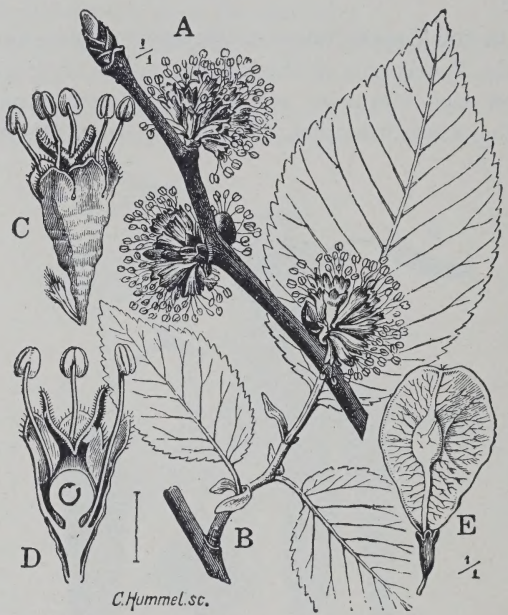


FIG. 465.—Flowers and fruit of elm (*Ulmus campestris*). A, twig at the time of blooming. B, twig with developed foliage leaves. C, a flower in side view. D, the same in longitudinal section. E, fruit. The flowers of the elm are perfect (monoclinous) with a bell-shaped calyx and 4 to 9 stamens; ovulary 1–2 celled; styles 2. (After Wossidlo.)

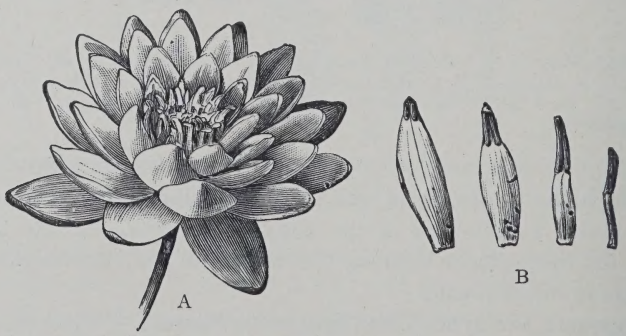


FIG. 466.—A, flower of white water lily (Castalia). B, parts of the flower, showing transition from stamens to petals. (Atwood.)

The Flower of the Compositae.—The highest degree of development in the dicotyls is regarded as having been attained in the Compositae, while that in the monocotyls is found in the Canna and in the orchid families.

The flowers of the Cichoriaceae and Compositae are usually borne in heads as in the dandelion and sunflower. Here the greatest degree of

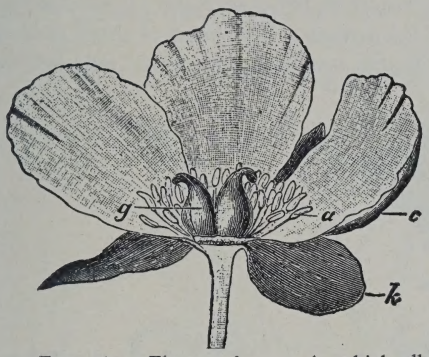


FIG. 467.—Flower of peony in which all the floral parts are attached separately to the torus; *k*, sepals; *c*, petals; *a*, the numerous stamens; *g*, the carpels. (After Strasburger.)

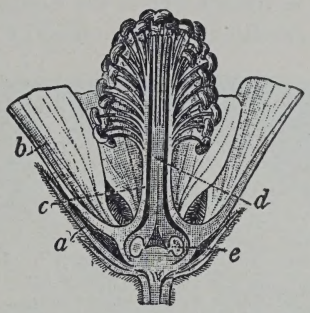


FIG. 468.—Flower of Althea halved longitudinally. *a*, sepals; *b*, petals; *c*, tube of stamens enclosing the style, *d*. (After Berg and Schmidt.)

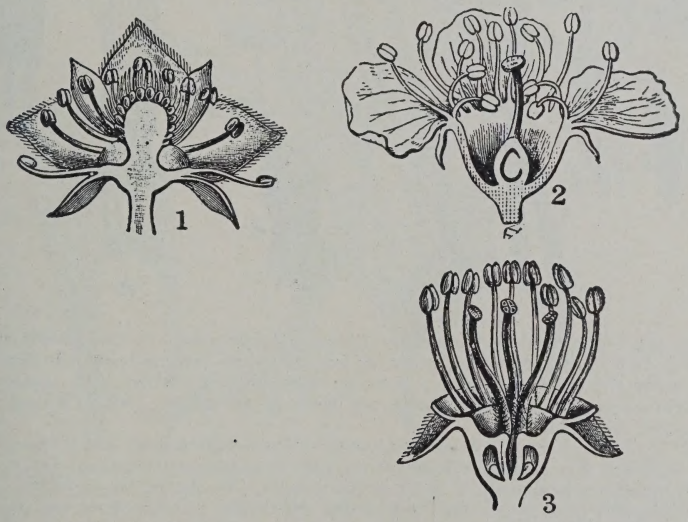


FIG. 469.—Flowers of the Rose family halved longitudinally. 1. hypogynous flower (*Potentilla palustris*), stamens, petals, and sepals arising from beneath the head of carpels. 2, a perigynous flower of the cherry (Prunus), stamens, petals, and sepals arising from the rim of the urn-shaped prolongation of the receptacle, which surrounds the carpel. 3, an epigynous flower of the apple in which all parts seem to arise from the top of the ovulary, two of whose cavities or "cells" are seen. (1, 3, after Focke.)

union has taken place. All parts are united from an early stage in development. The calyx is adnate to the ovulary, and when visible is termed the pappus. The five petals are united into a corolla of one piece, and

inserted on it are the five stamens, whose anthers are united in a tube (syngenesious) around the style.

These features are nicely illustrated in the dandelion (Cichoriaceae) and in Arnica, one of the Compositae proper. The head of the flowers in the dandelion is surrounded by a double involucre, the outer reflexed, the

FIG. 470.

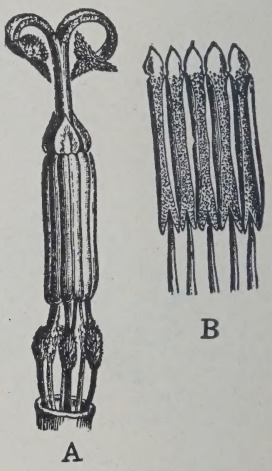


FIG. 471.

FIG. 470.—The common dandelion (*Taraxicum officinale*). 1, two flower stalks; in one the head is closed, showing the double involucre, the outer reflexed, the inner erect; in the other the head is open. 2, a single flower. 3, a mature fruit, *achene*. 4, a receptacle from which all fruits save one have fallen away. (After Wassidlo, from Strasburger, Macmillan Co.)

FIG. 471.—Stamens of a flower of Cosmos (*Cosmos bipinnatus*), one of the sunflower family. A, the five anthers united into a tube (syngenesious) around the style; the separate filaments bear tufts of hairs at the middle. B, the anther tube has been slit at one side and opened out flat; seen from the inside. Connectives are prolonged; dehiscence longitudinal. × 7. (From Baillon's, "History of Plants," Librairie Hachette.)

inner erect (Fig. 470, 1). The tubular corolla of five petals is spread out above into a flat piece, the ligule (2). All the flowers of the dandelion are ligulate. The ovulary is prolonged into a beak ending in a crown of bristles, which represents the calyx (Fig. 470, 2). The tube formed around the style by the adhering anthers is clearly shown in Fig. 471, A, B. The anthers open longitudinally on the inside. The pollen is consequently

shed in the tube and swept out by the brush-like hairs of the style as it elongates. The stigmas may then curve outward and downward and come in contact with the pollen (Figs. 471, A and Fig. 473, B, C).

FIG. 472.—Part of a specimen of Arnica (a plant similar to the common daisy) A, lower and upper parts of stem, the latter bearing a head of ray and disk flowers B, a single ray flower showing the corolla, tubular at the base and strap-shaped (ligulate) above, the two parted style, the tuft of pappus hairs (calyx), and the inferior ovary. C, single disk flower with tubular corolla and spreading lobes of the petals. D, inner view of stamen. (After Hoffman from Coulter's "Plant Structures," D. Appleton & Co.)

The head of flowers of Arnica, a plant like the daisy, which is surrounded by an involucre of leaf-like bracts, consists of two forms of flowers. Those around the margin, the ray flowers, have ligulate corollas, as in the dandelion (Fig. 473, A). The ray flowers of Arnica are pistillate only. Within the circle of ray flowers is the broad disk containing

numerous tubular, monoclinous flowers, the disk flowers. If a disk flower be removed, it will be seen that a tuft of delicate hairs, the *pappus*, arises from the ovulary around the tubular corolla (Fig. 473, B, C).

The pollen is shed in the tube, as in the dandelion, and brushed out by the elongating style. Fig. 473, B, C, shows the manner in which the bifid style curves to bring the stigmas in contact with the pollen.

In some Compositae (Centaurea and Cyanus) the marginal flowers may be completely sterile, functioning only to render the head conspicuous to insects.

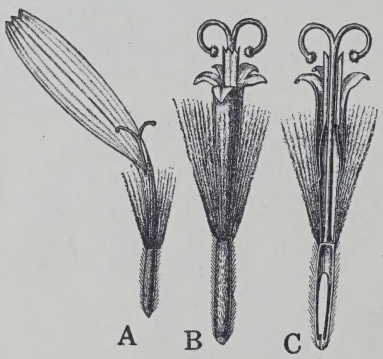


FIG. 473.—Flowers of *Arnica montana*. *a*, ray flower; *b*, disk flower; *c*, disk flower in longitudinal section. (After Berg and Schmidt.)

FIG. 474.—Flower of Canna (*Canna iridiflora*). *f*, ovulary; *k*, calyx, *c*, corolla; *l*, the lip or labellum; *a*, fertile stamen; *g*, style; *st*, 1, 2, 3, the staminodia. (Strasburger, Macmillan Co.)

In the monocotylous plants, the flowers of Canna and the orchids are highly specialized. In the flower of the Canna, commonly cultivated in our parks and gardens, (Fig. 474) five of the stamens are changed into petaloid *staminodia*, which form the showy part of the flower, the perianth being inconspicuous. The sixth stamen is also petaloid, bearing pollen upon one side, i.e., only one half of the anther producing pollen (*a*). The labellum (*l*) represents two staminodia (Detailed explanation in legend of Fig. 474).

The remarkable flower of Orchis is zygomorphic (Fig. 475, A). The perianth is petaloid. The posterior segment (petal) of the inner circle is changed into the lip (*e*) which frequently develops a spur (*f*). The lip

(labellum) becomes anterior by the twisting of the flower through 180° or by the flower being bent backwards. The androecium is formed of the three anterior stamens only, the middle stamen, belonging to the outer circle, bears pollen; the other two are changed to staminodia (B, *p*). The pollen bearing stamen is united to the style and forms the *column* (gynostemium) (A, *g*). This structure projects into the center of the flower. The two pollen masses are each provided with a stalk ending in a

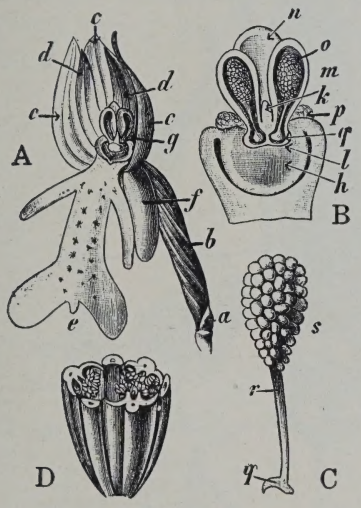


FIG. 475.

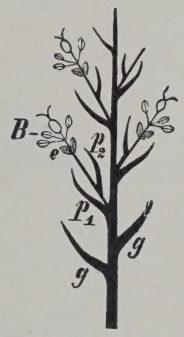


FIG. 476.

FIG. 475.—Flower of an orchid (*Orchis militaris*). A, *a* bract; *b*, ovulary; *c*, the outer, and *d*, the two anterior perigone leaves; *e*, the lip (labellum) with spur, *f*, (nectary); *g*, the gynostemium, the union of stamens and pistil. B, flower after removal of all of the perigone leaves with the exception of the upper part of lip; *h*, stigma; *l*, rostellum, a beak-like extension from the upper edge of the stigma; *k*, tooth-like prolongation of rostellum; *m*, anther; *n*, connective; *o*, pollinium; *q*, viscid disk; *p*, staminodium. C, a pollinium removed and enlarged; *r*, its stalk (caulicle); *s*, pollen mass. D, ovulary in cross section.

FIG. 476.—Diagramatic representation of a grass spiklet of three perfect flowers. *g*, sterile glumes; p_1, lemma (inferior flowering glume); p_2, palea, sometimes called the palet (superior flowering glume); B, the flower consisting of tree stamens and a pistil and two lodicules, *e*. The axial parts are represented as greatly elongated. (Strasburger, Macmillan Co.)

sticky disk which adheres to the head of a visiting insect (Fig. 475, C, *q*). More detailed explanation is given in the legend of Fig. 475.

The Flower of a Grass.—The typical grass flower is simple, consisting of a pistil with two feathery stigmas and three stamens. The unit of arrangement in grass flowers is the spikelet, and we may first become acquainted with the spikelet, using a diagram in which the axial parts are represented as greatly elongated (Fig. 476). A spiklet bears one to several flowers. At the base of the spikelet there is usually a pair of

empty bracts, *glumes* (Fig. 476, *g*, *g*). One or both glumes may be rudimentary or absent. Following the glumes, come the two bracts which enclose each flower. The lower bract, p_1, is the *lemma*, in the axile of which stands the flower; the upper bract is the *palea*, p_2. Above the

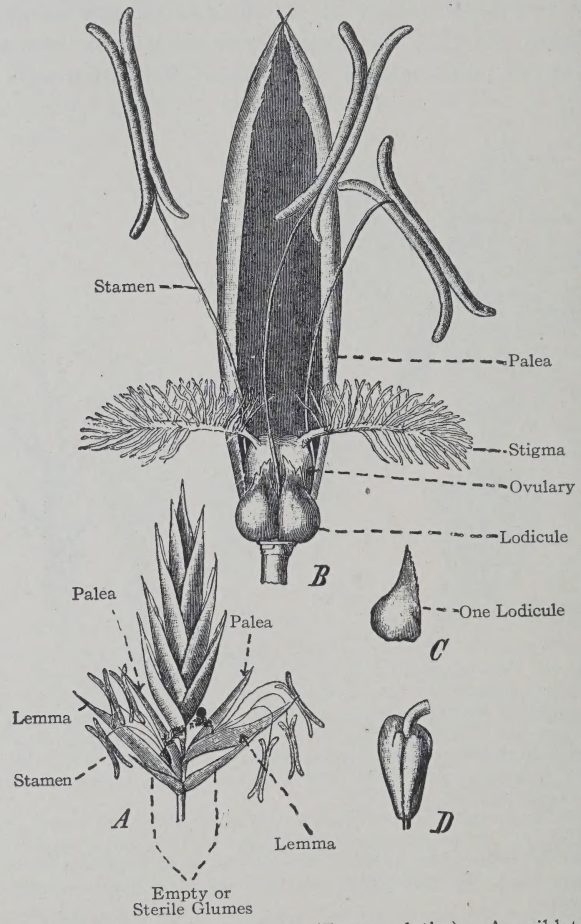


FIG. 477.—Spiklet and flowers of a grass (*Festuca elatior*). A, spiklet with the two lower flowers open, below which the two sterile glumes are shown (× 3). B, flower with the palea behind it and the two lodicules in front, lemma removed; the ovary bears two feathery stigmas (× 12). C, one lodicule (× 12). D, ovary seen from the side with the stalk of one of the stigmas (× 12). (Strasburger, Macmillan Co.)

palea, come the two *lodicules* (*e*) which on being distended assist in opening the flower. Lastly the delicate axis bears the flower (B) consisting of a whorl of three stamens and a pistil. The ovulary, consisting of one carpel, bears two feathery, papillose stigmas. The lemma is often awned, i.e., it may bear a stiff bristle (*awn*) with backward pointing hairs.

In the actual spikelet the axes are very short. Fig. 477, A represents a spikelet of the fescue grass (*Festuca elatior*) enlarged three times. Two flowers below are open. At B is shown one flower with two lodicules in front and the palea behind, the lemma having been removed (enlarged 12 times).

Flowers in some grasses are not so greatly reduced. In the rice, the flower has a complete androecium of six stamens; that of the Bambuseae is similar, and has three lodicules. The grass, Streptochaeta, has a normal monocotylous type of flower. In some grasses the flower has a larger number of stamens.

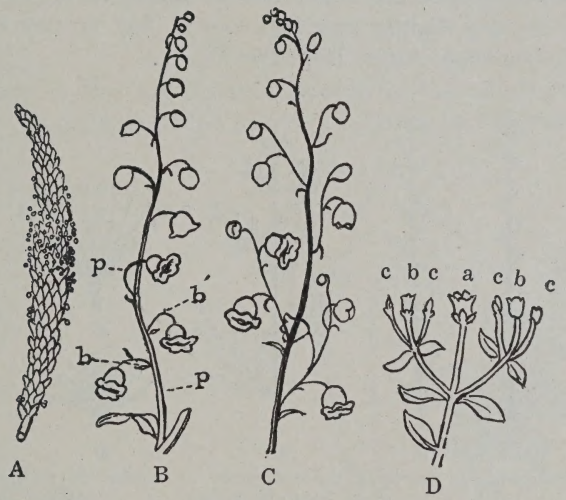


FIG. 478.—Inflorescences. A, spike. B, raceme. C, panicle. D, cyme. *p*, peduncle; *p'* pedicel; *b*, bract; *b'* bractlet; *a*, oldest flower of cyme; *b*, *c*, successively younger flowers.

Sedges.—In general appearance sedges are grass-like plants. The stems, as a rule, are not hollow and jointed at the nodes as are those of grasses. Save in the rush-like sedges (Scirpus), the stems are usually triangular. The flowers are similar to the grasses. Each is borne in the axil of a chaff-like bract. Lemma, palea, and lodicules are lacking. A few hypogynous bristles may take the place of a perianth.

Arrangement of Flowers, Inflorescence.—The manner in which flowers are arranged upon the primary axis is referred to as the inflorescence. In a broad sense there are two types of infloresences: the *racemose*, (indeterminate) in which the terminal or central flowers are the younger, the older flowers being at the base of the axis; and the *cymose* (determinate), in which the terminal or central flower is the oldest. In a racemose

inflorescence the succession of development is centripetal, while that in the cymose is centrifugal.

Racemose Inflorescences.—Of this type of inflorescence the following are the most common:

Spike.—In the spike the axis (rhachis) is slender, and the flowers are sessile, i.e., with a very short or scarcely perceptible pedicel (Fig. 478, A). The common plantain is an example.

Spadix.—In the spadix the flowers are sessile, and the axis generally thick and fleshy. The jack-in-the-pulpit is a good illustration (Fig. 457). The leaf-like structure which surrounds the spadix is the *spathe.*

Head.—In the head the sessile flowers densely cover the receptacle, which may be very slightly tapering, conical, flat, or even hollowed out (red clover, dandelion, Aster) (Fig. 479, D).

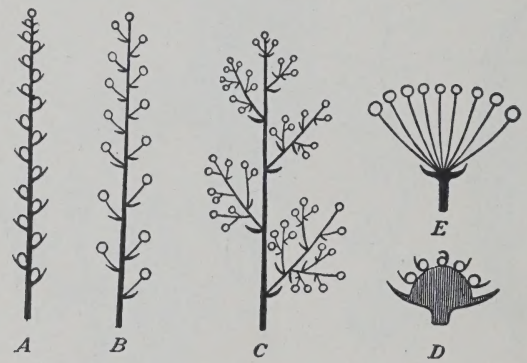


FIG. 479.—Diagrams of racemose inflorescences. A, spike; B, raceme; C, panicle; D, head; E, umbel.

Raceme.—In the raceme the flowers are all definitely stalked, and may be subtended by bracts. A typical raceme is found in the lily-of-the-valley and in the shepherd's purse (Fig. 478, B).

Corymb.—A corymb is a flat-topped raceme. The flowers are arranged as in a raceme, but the pedicels of the lower flowers are longer than those of the upper, so that all the flowers are borne at approximately the same level, a flat-topped cluster as in the hawthorn.

Umbel.—In the simple umbel the flowers are all stalked in a rosette and spring from a short rhachis. The flower stalks are arranged somewhat like the braces of an umbrella, as in the wild carrot (Fig. 479, E).

Panicle.—A panicle arises when the lateral branches of the primary axis, or branches of the first order, also branch (Fig. 478, C). There are various forms of complicated panicles, such as those composed of small spikes, as in some species of Spirea, in the inflorescences of wheat, oats,

rye, etc. In Fig. 479, the above racemose inflorescences are illustrated in diagrammatic form.

Cymose Inflorescence.—As stated in a preceding paragraph, a cyme results when the primary axis terminates in the first and oldest flower (Fig. 478, D.). The primary axis branches immediately beneath the pedicel of the first flower in such a manner that each lateral axis terminates in a flower after producing one or more lateral axes. The later axes also terminate each in a flower and they may continue the system in a similar manner. The inflorescence of the common wild rose (*Rosa setigera*) is a typical illustration. In the tulip we have a cyme bearing one flower. There are various complicated forms of cymose inflorescences.

Pollination

Pollination in the Angiosperms consists in the transferral of pollen from anther to stigma. If the pollen of a flower be deposited upon the

Fig. 480.

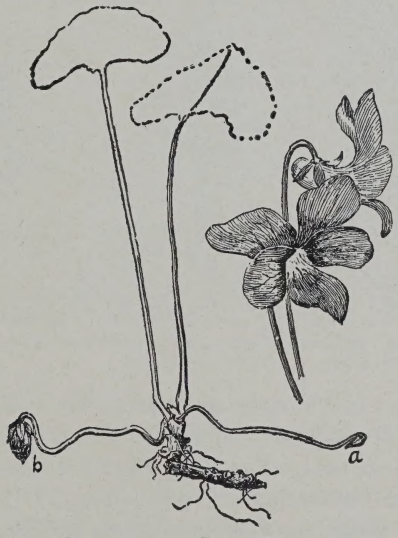


Fig. 481.

Fig. 480.—Adaptation for self-pollination in the common mallow (*Malva rotundifolia*). The stigmas when mature curl downward among the stamens.

Fig. 481.—Cleistogamous flowers of the common blue violet, reduced. The cleistogamous flowers are borne on branches close to the ground. *a*, a small flower; *b*, fruit from a similar flower. At the right two ordinary flowers. (From Bailey, "Encyclopedia of Horticulture," Macmillan Co.)

stigma of the same flower, or upon that of another flower of the same plant, *self pollination* is effected. When, however, the pollen of one plant is deposited upon the stigma of another plant, *cross pollination* is accomplished.

Self Pollination.—In many plants the anthers of the flower are in such a position that, on opening, the pollen will be applied to the stigma. The stigmas and stamens may develop in such a manner as to insure self pollination, even though cross pollination may also occur. This is illustrated in the common mallow as shown in Fig. 480. Here the stigmas and stamens mature at the same time, the former curling downward among the numerous stamens.

Cleistogamous Flowers.—Certain flowers of some plants do not open at all, and self pollination necessarily takes place. Such flowers are termed *cleistogamous*. The common blue violet bears two kinds of flowers. Early in the season the large familiar, showy flowers are produced upon long pedicels, over-topping the leaves (Fig. 481, right). Later in the season very small flowers are developed near the ground (Fig. 481, *a*, *b*). When the anthers open the pollen comes in direct contact with the

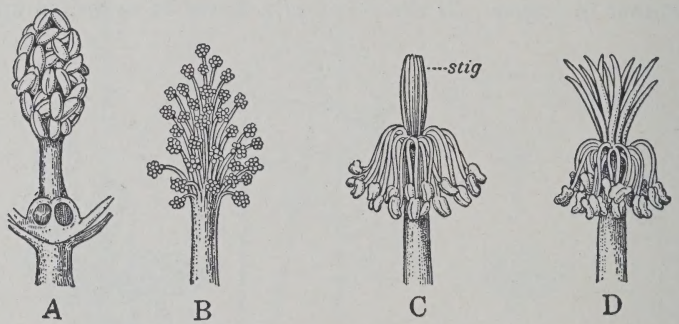


FIG. 482.—Adaptation for cross pollination in the mallow, *Malva sylvestris*. A, position of stamens and pistil in the bud. B, the mature stamens discharging pollen. C, stamens reflexed, stigmas (*stig*) still immature. D, stigmas ripe and separated, anthers withered. (After H. Muller.)

stigmas. In the cleistogamous flower a very small quantity of pollen is developed and little is needed. The blue flowers which open may or may not produce seed, while those which are cleistogamous almost always do so.

Cross Pollination.—Cross pollination presents a wide range of phenomena which are most interesting and fascinating because of the varied agencies concerned and because of the adjustments between the flowers and the pollinizing agency. In many flowers which are adapted to cross pollination, self pollination is prevented in various ways, such as in dioecism, and in the maturing of stamens and stigmas at different times. Or, it may happen that the position of anthers and stigmas may be such that self pollination is effectively prevented. If the anthers mature before the stigmas, the flowers are said to be *protandrous;* if stigmas mature before the pollen is ready, *protogyny* results. Each condition is efficient in preventing self pollination. The dwarf larkspur (*Delphinium tricorne*)

and the garden Nasturtium (*Tropaeolum*) are illustrations of protandry, while in the common plantain we have a good example of protogyny. The flower of the tall mallow affords an excellent illustration of the effectiveness of protandry. In Fig. 482, A, the stamens and pistil are shown as they are in the bud. In B the stamens are shedding the pollen. In C the anthers are reflexed, but the stigmas are not mature, and in D the stigmas are ready but the anthers are withered.

Attention has already been directed to another species of mallow (Fig. 480) in which stamens and stigmas are so developed that self pollination is unavoidable.

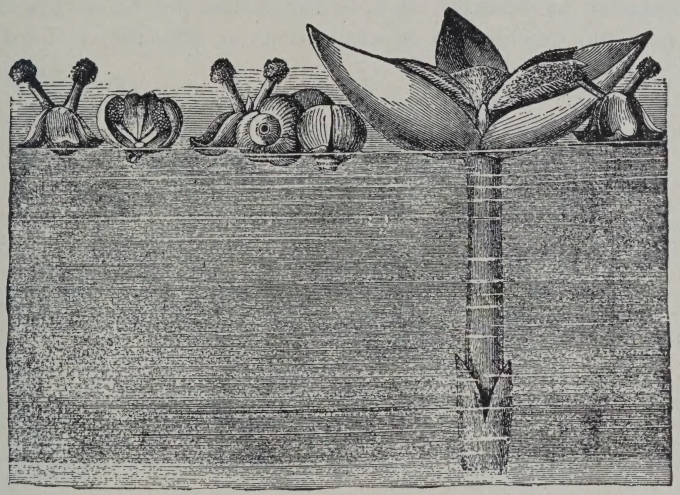


FIG. 483.—Pollination of eel-grass (*Vallisneria spiralis*). The large flower is a pistillate one near which are floating the small staminate flowers in different stages of maturity. The ones at the right and left are fully open. They float upon the reflexed boat-shaped lobes of the perianth; the one at the right has floated so that the pollen is brought in contact with the fringed stigma of the pistillate flower. ×10 (see Fig. 521). (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

Agencies of Cross Pollination.—The agencies of cross pollination in nature are wind, water, and animals (chiefly insects). Humming birds may also pollinize certain flowers.

Wind.—Currents of air are doubtless the most effective agencies in bringing about pollination through long distances. Wind pollination occurs in most of our forest trees, e.g., in alders, birches, oaks, hickories, walnut, elms, in some of the grasses, including Indian corn, and in some herbaceous plants. Wind pollinized plants produce dry pollen in great abundance. The flowers are diclinous, the staminate being far more numerous than the pistillate. In dioecious species, staminate and pistillate individuals may be far removed from each other, yet, owing to the great

abundance of dry pollen, the stigmas of isolated trees are likely to be pollinized.

Water.—In certain aquatic plants, such as Elodea, Naias, and Vallisneria, pollination takes place on the water. The eel-grass, Vallisneria, will serve as an illustration. The plant grows in masses beneath the surface of the water and produces, upon long stalks, the pistillate flowers which float at the surface. The very small staminate flowers, borne submerged, are set free and rise to the surface. They float about, and, when they come in contact with a pistillate flower, an anther is likely to touch a feathery stigma, as shown in Fig. 483, right.

Pollination by Insects.—It is in the pollination by insects that the most manifold and marvelous adaptations or adjustments between the

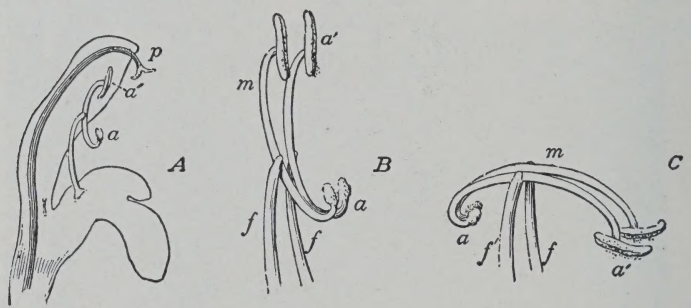


FIG. 484.—The flower and stamens of the common sage (Salvia). A, a flower halved lengthwise and seen from one side; *p*, stigma; *a*, *a'*, anther. B, the two stamens greatly enlarged, in the normal position in the flower; *f*, filaments; *m*, connective; *a*, *a'*, cells of anther. C, the anthers and connectives bent into a horizontal position by an insect pushing against *a*. (After Lubbock.)

flower and its pollinizing agency are encountered. Insects visit flowers to secure food in the form of pollen and nectar, to deposit their eggs, to seek shelter, or for reasons unknown. The nectar is produced by glands located in the flower or near the flower. The pollen of flowers pollinized by insects may be dry and powdery or sticky, or it may adhere in masses provided with sticky disks, as in orchids, or with a clip-like device by which the masses adhere to certain parts of the insect's body, as in the common milkweed (Asclepias).

In order that the visit of an insect may result in successful cross pollination, that portion of its body, to which the pollen adheres when a visit is made, must be brought in contact with the stigma of another visited flower. In general the position of anthers and stigmas is such that the insect, in making its visit, will become dusted with the pollen or will brush or touch the stigma with the pollen laden portion of its body with almost unerring certainty.

Illustrations of the foregoing statements are found in the flowers of many plants. We shall select the common sage as one in which the structure of the flower and its adaptation to pollination by insects is of unusual interest. In Fig. 484, A is shown a flower halved lengthwise. It has two peculiar stamens (B) with rather short filaments (*f*, *f*) and unusually long connectives (*m*). One half of the anther (*a'*) bears pollen, the other half (*a*) at the opposite end of the long curved connective is sometimes sterile. An insect visiting the flower to sip the nectar pushes its head against *a* bringing the anthers to a horizontal position (C). The result is also shown in Fig. 485, A, B, C, D, E, with the arrow point indicating the thrust of the bee. The style lies close to the upper lip

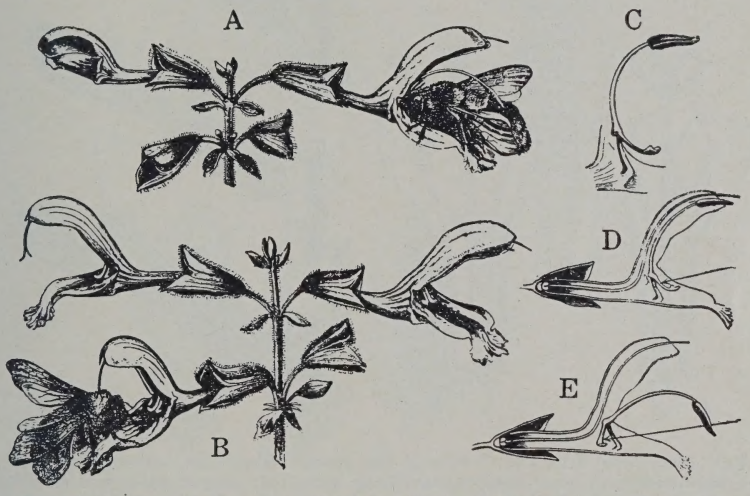


FIG. 485.—Pollination in the sage (Salvia). Explanation in text. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

of the corolla following its curve, the stigma projecting slightly from the tip of the upper lip (A, B, at the right). In this condition the pollen is ready, since the flower is protandrous. The bee visiting such a flower pushes against the sterile part of the anther, and the fertile part strikes the insect's back, depositing pollen (A, at the right). As the flower becomes older, the style lengthens and curves downward, bringing the stigma to the position shown in the upper left flower in B. The bee visiting such a flower is shown at the left below. The stigma brushes against that part of its body dusted with pollen.

Another remarkable adaptation for cross pollination occurs in those plants in which different forms of flowers are present, and in which there is a difference in pollen also. The bluet, (Houstonia) is an illustration. Here, some flowers have short stamens and long styles, others long stamens

and short styles (Fig. 486, A, B). Moreover the pollen produced by the short stamens is functional chiefly upon the stigma borne by the short style, and that of the long stamens is functional upon the stigma of the long style. An insect, visiting such flowers, will make the legitimate crosses, namely, long stamen pollen to stigma of long style, and short stamen pollen to stigma of short style.

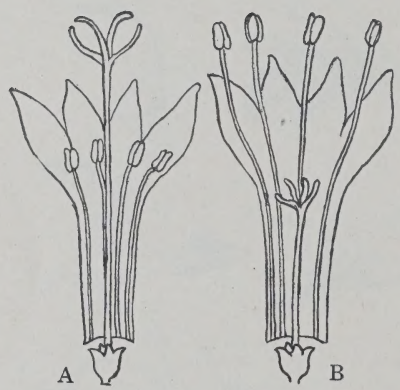


FIG. 486.

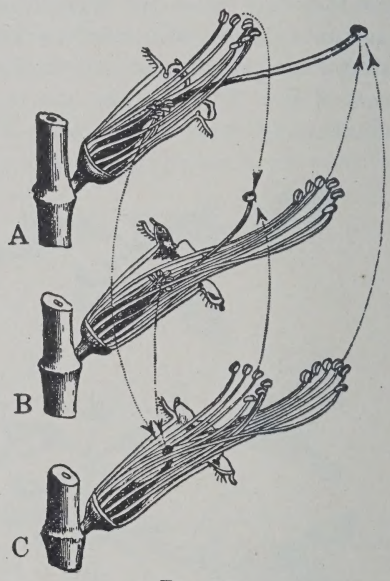


FIG. 487.

FIG. 486.—Two forms of flowers of the bluets (Houstonia) opened out and seen from the inside. A, short stamens and long style. B, long stamens and short style. An insect visiting A will receive pollen upon the front part of its body; upon visiting B this pollen will rub against the stigmas, and the pollen from this flower will be received by the under part of the body; upon visiting another flower like A, the pollen from B will be brushed against the stigma of A.

FIG. 487.—The three forms of flowers in the loosestrife, (*Lythrum salicaria*). The corollas and calyces are omitted in order to show the different lengths of stamens and styles. The functional crosses are indicated by the arrows. (From Darwin's "Cross Pollination," Courtesy of D. Appleton & Co.)

In some cases, three forms of flowers are present, as in the loosestrife (*Lythrum salicaria*). Each flower has stamens of two lengths, which, with the style, make possible three combinations (Fig. 487). One flower has short stamens, middle-length stamens and long style (A); another has short stamens, middle-length style and long stamens (B); the third has short style, middle-length stamens, and long stamens (C). In all these cases pollen is supposed to be potent upon stigmas borne by styles of the same length as the stamens. The proper crosses are indicated by the arrows in Fig. 487.

Pollination in Yucca and in the Fig.—In two plants, the Yucca and the Fig, there is a special relation between each plant and a certain insect which is the sole pollinizing agency for that plant.

In the Yucca the larva of a snowy-white moth (Pronuba) one-half inch in length is nurtured in the developing fruit (Fig. 488, C, D). When fully matured the moth may be found during the day resting in the flower. At sundown or a little later she begins work. She climbs upon an anther and, by means of her mouth parts, gathers a tiny ball of pollen, as shown in Fig. 488, B. She then takes a position like that in A, and deposits an

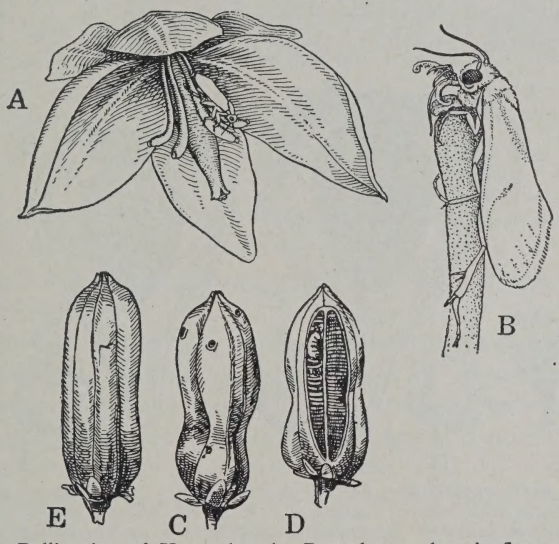


FIG. 488.—Pollination of Yucca by the Pronuba moth. A, flower in which the moth is depositing eggs. B, moth gathering pollen. C, a pod developed as a result of pollination by the insect; note the holes through which the larvae have escaped. D, younger pod with part of wall cut away, showing larva among the seeds. E, pod resulting from hand pollination. (Folsom.)

egg or eggs in the ovulary of the flower. Following oviposition she ascends the pistil and rubs the pollen upon the stigma, apparently as if she did so consciously. This is the only way in nature by which the plant is pollinized. If pollination is done by hand the developed fruit will appear like that in Fig. 488, E. A fruit developed following pollination by the moth will appear much as in Fig. 488, C.

From the egg deposited in the ovulary the larva will develop, feeding upon the tender growing seeds (D). There are many more developing seeds than all the larvae in the pod can consume, so that seed production is interfered with to a small extent only. When the larva is fully developed it makes a hole in the wall of the fruit and escapes into the ground where the winter is spent. The insect does her work through

instinct. She does not reason about it. How the habit was acquired nobody knows.

The story of the relationship between the fig and the very small wasp (Blastophaga) which effects pollination, is extremely interesting. The flowers of the fig are borne in a peculiar way. The structure called a fig is a hollow, pear-shaped enlargement of the end of a branch (Fig. 489, A, B), completely closed save for a small opening at the top, and bearing numerous small flowers upon the inner wall. The fig is really an inflorescence. Figs are dioecious, so that some trees bear figs with functional staminate flowers (Fig. 489, B, C), and others, figs with functional pistillate flowers (Fig. 489, A, E). The sterile

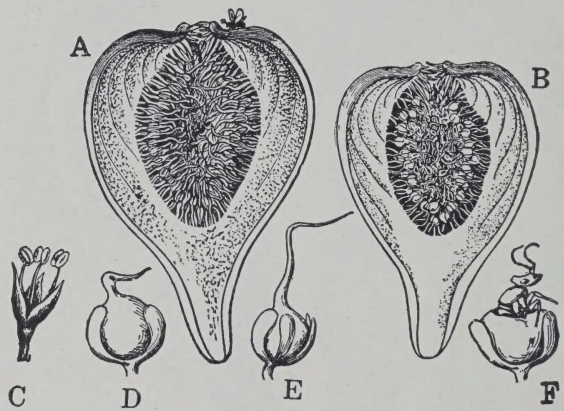


FIG. 489.—Inflorescences and flowers of the fig tree. A, a young pistillate (seed-producing) inflorescence halved lengthwise. Note the wasp ready to enter and the one which has just entered. B, a similar section of a staminate inflorescence with numerous sterile pistillate flowers (gall flowers) in which young wasps are developing. C, a functional staminate flower. D, a sterile pistillate (gall) flower with short style (insect developing within). E, a fertile pistillate flower with long style. F, a wasp emerging from a sterile pistillate flower. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

pistillate flowers in the fig which bears functional stamens do not set seeds, but they nurture the fig wasp. They have short styles (Fig. 489, D), whereas the functional pistillate flowers have long styles (Fig. 489, E). The tree that has been cultivated for centuries along the Mediterranean is the pistillate tree. In order that they may bear the juicy, and well flavored Smyrna figs, it was necessary to hang upon the branches of the trees, twigs bearing functional staminate flowers. These staminate figs were called "wild figs," or "*caprifigs*," and the process of placing them on the pistillate tree was called *caprification*. Caprification was carried on for centuries before its real meaning was known. In recent years the meaning of the process has become known. Inasmuch as the trees are functionally dioecious, caprification consists in bringing staminate flowers

near enough to the pistillate flowers so that pollination may take place. As both kinds of flowers are enclosed in the fig, it is evident that neither wind nor ordinary insects could transfer the pollen. The functional pistillate figs, i.e., those which produce the fine fruit, set seeds, while from the ovularies of the caprifigs come the tiny wasps (Fig. 489, D, F) which spend their entire lives in the figs. The female wasp when mature becomes dusted with pollen in her efforts to escape from the old fig. Having escaped from her home she flies to a nearby younger fig and enters through the small opening to deposit her eggs (Fig. 489, A). If she enters a pistillate fig, some of the pollen is deposited upon the stigmas and seeds will be developed, but she leaves no progeny in such figs, for the reason that the long style (Fig. 489, E) prevents the egg from being deposited properly to develop. In the staminate, or caprifigs, on the contrary, the style is short, and the deposited egg develops into the insect (Fig. 489, D, F).

The male wasps die in the figs in which they were born, and the females die in the figs in which they deposit eggs.

The wasp is a weak flying insect, and caprification increases her chances of entering the tame fig.

The life history of the wasp is repeated over and over again. Each new generation of females creeps out of the old fig, enters another that is younger, deposits eggs and dies. A staminate tree bears two or three crops of caprifigs each year, and there is always a home for the two or three generations of wasps produced each year.

During the last few years of the past century the United States Department of Agriculture, after a number of failures, succeeded in introducing the fig wasp into California, so that real Smyrna figs are now grown in our country.

The Fruit.—In a purely botanical sense a fruit is the matured pistil. The term is sometimes extended to include accessory and other parts, such as the axis, receptacle, or involucre, especially if those parts become succulent, brightly colored or pulpy. Seeds may or may not be present.

The development of the fruit begins immediately following pollination, so that seeds and fruit reach maturity at about the same time. The growth of the pistil into the mature fruit is very rapid in many plants, the size of the fruit often becoming enormous in comparison with the size of the pistil in the flower. One has merely to recall the size of the pistil in the flower of the pumpkin or of the watermelon to realize the enormous growth of the pistil following pollination.

If the wall of the ovulary and adhering parts become dry, membranous or woody, dry fruits result. If the ovulary and adhering parts become succulent or pulpy, the term fleshy fruit is applied.

The wall of the ovulary in the fruit becomes the *pericarp*. The pericarp may differentiate during development into two or three layers. The outer layer is the *epicarp* (sometimes merely an epidermis), and the inner part is the *endocarp*. Between these two there may be a third layer, the *mesocarp*. For example, in the peach, plum, and cherry, there is a thin epicarp, a thick pulpy mesocarp, and a stony endocarp.

Dry Indehiscent Fruits.—In dry indehiscent fruits the pericarp does not open, but closely envelops the seed until germination. The seed coat is thin and membranous. The following are examples:

The Achene.—An achene is a small one-celled, one-seeded, dry indehiscent fruit, as in the dandelion, sunflower, Aster.

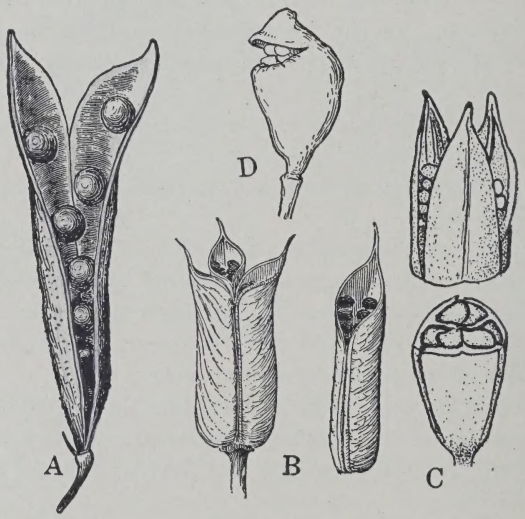


FIG. 490.—Dry dehiscent fruits. A, legume of sweet pea. B, a cluster of three follicles and a single follicle of monkshood. C, capsule of Iris dehiscing. D, capsule of *Jeffersonia diphylla* opening by a lid. (B, after Faguet.)

A Caryopsis.—A caryopsis is a kind of an achene. The grains of Indian corn, wheat, etc., are examples. Here the pericarp is thin and tough, closely investing the seed and adhering to the seed coat. In a true achene the pericarp is separable from the seed coat.

The Nut.—In the nut the pericarp is tolerably thick, stony, or woody. Examples are the hazel nut, chestnut, and beech nut. The husk about each of these fruits is an involucre (Fig. 459, 460).

Samara and Schizocarp.—These are bilocular or plurilocular, dry indehiscent fruits. They usually separate into mericarps. In the *schizocarp*, as in the carrot, parsnip, and other members of the Umbelliferae and in certain species of the geranium family, each mericarp resembles a

nut or achene. In the samara (Fig. 505), the fruit of the maple, the mericarps are winged.

Dry Dehiscent Fruits.—In dry fruits that open to release the seeds, the pericarp splits in various ways. In such fruits, the seeds possess well-

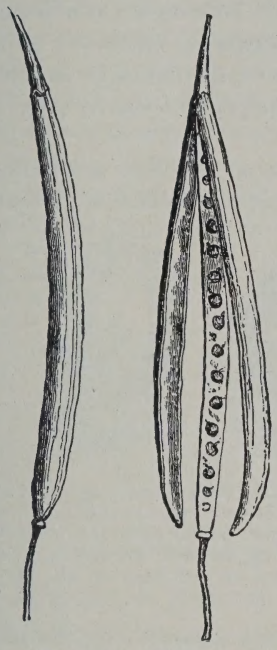


FIG. 491.—Closed and open silique of cabbage, a member of the mustard family (Cruciferae). (After Warming.)

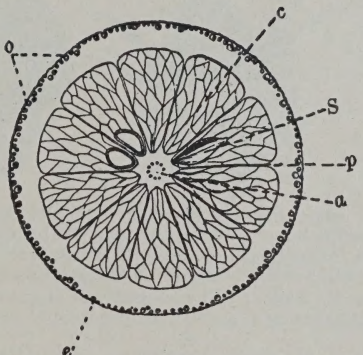


FIG. 492.—Cross section of an orange, a kind of berry. A, axis of fruit; *p*, partition between cells of ovulary; *s*, seed; *c*, cell (loculus) of ovulary filled with pulp composed of sacs filled with juice; *o*, oil reservoirs near surface of rind; *e*, firm outer layer of rind. (From Bergen & Davis, "Principles of Botany," Courtesy of Ginn & Co.)

developed hard or tough seed coats. Among the dry dehiscent fruits are the following:

Follicle.—A follicle (Fig. 490, B) consists of a single carpel which opens along the adaxial (inner) suture (common milkweed, larkspur, monkshood, and peony).

Legume.—A legume consists of a single carpel which opens along both the adaxial suture and the median, abaxial (outer) line; it separates into longitudinal halves (Fig. 490, A). Examples are the pods of peas, beans, redbud, black locust.

Capsule.—The term, capsule, is often used in a very broad sense. In the narrower use of the word, a capsule is a fruit developed from a compound ovulary (unilocular or plurilocular) which splits longitudinally into two or more valves from the top downwards, as in chickweed (Cerastium), Iris, tulip, jimson weed. If the longitudinal fissures pass through the partitions, the dehiscence is *septicidal*, but, if the fissure is in the middle between each pair of partitions, the dehiscence is *loculicidal*, as in the garden tulip and Iris (Fig. 490, C). Some capsules open by an uplifting lid, as in Jeffersonia (D). The capsule of the poppy opens by pores at the top.

Silique or Silicle.—The silique is typical of the fruit in the mustard family (Cruciferae). It consists of a compound ovulary of two carpels,

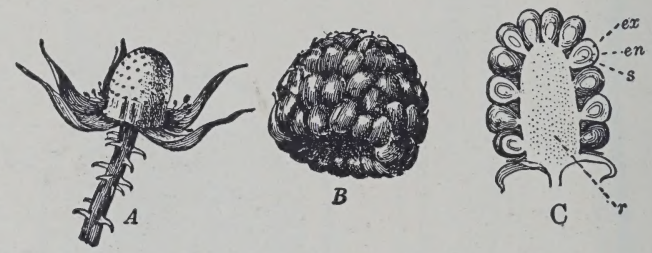


FIG. 493.—Fruit of raspberry and blackberry. A, flower stalk, calyx, old stamens and receptacle from which the fruit (B), a cluster of druplets, has been removed. B, the cup-shaped mass of removed drupelets. C, longitudinal section of a blackberry; *r*, the fleshy axis to which the drupelets adhere; *ex*, exocarp; *en*, endocarp; *s*, seed. (A, B, from Bailey, "Encyclopedia of Horticulture," by permission of The Macmillan Co., Publishers.)

and it opens longitudinally by two valves which separate from the partition (Fig. 491).

Succulent Indehiscent Fruits.—In this class of fruits the pericarp or certain of its layers remain pulpy. Those commonly met with, are the drupe, berry, and pome.

The *drupe*, or *stone fruit*, has a thin epicarp, a fleshy mesocarp and a stony endocarp enclosing the seed which has a thin seed coat, as in the plum, peach, cherry.

The *pome* consists of a tough epicarp, a pulpy or succulent mesocarp, and a leathery or bony endocarp. The apple and pear are typical pomes.

The *berry* has a more or less firm or tough epicarp and a pulpy mesocarp in which the seeds are embedded. Examples are the grape, tomato, currant, gooseberry. The fruit of the cucumber, pumpkin and melons is called a *pepo*.

The Orange, Lemon, Grapefruit, and Other Citrous Fruits.—Allied to the berry are the citrous fruits. Here the pericarp consists of a tough outer layer, the rind, a pith-like center and between these two the very

juicy pulp containing the seeds when they are present (Fig. 492). The pulp develops as follows: from the innermost layer of the plurilocular ovulary, protuberances are developed at an early stage which fill the loculi as isolated but closely packed masses of succulent tissue known as the pulp.

Aggregate and Accessory Fruits.—The blackberry, raspberry, mulberry and the strawberry, etc., belong to this class. The blackberry consists of a collection or aggregate of small drupes, or drupelets, which adhere to the enlarged and pulpy receptacle (Fig. 493, C). In the raspberry the collection of drupelets separates readily from the receptacle as a cup-shaped mass (Fig. 493, A, B).

Strictly speaking, the fruit of the mulberry tree consists of an achene covered by the calyx which becomes pulpy. The whole spike of pistillate

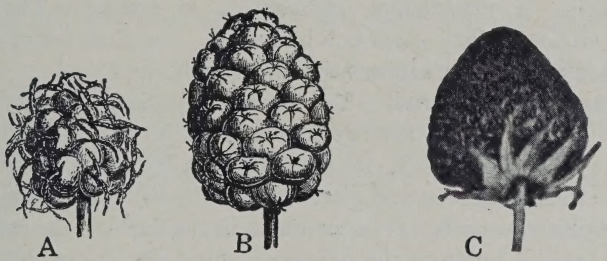


FIG. 494.—A, a cluster of pistillate flowers of white mulberry. B, aggregate fruit of the same. C, a strawberry, a reinforced or accessory fruit. (A, B, after Baillon.)

flowers (Fig. 494, A) gives rise to the collection of such achenes which we call the mulberry (B).

The *strawberry* is spoken of as an accessory fruit. It consists of a greatly developed, pulpy receptacle in the surface of which are located the numerous *achenes*, the *real fruits* (Fig. 494, C).

In the *pineapple* the whole flower cluster has become an enlarged fleshy mass including axis and bracts.

Succulent Dehiscent Fruits.—In this type of fruit the succulent, though not pulpy, pericarp bursts and discharges the seeds in which the seed coat is strongly developed. The fruits of the touch-me-not (Impatiens) and the buckeye are examples. The term succulent capsule is sometimes applied to these two fruits.

The fruit of the *black walnut* and of the *butternut* correspond to the drupe. The outer succulent layer or hull becomes broken and sloughs off or decays, exposing the stony endocarp enclosing the seed which has a very thin seed coat.

Special Kinds of Fruits, the Hickory Nut and Pecan.—In the hickory nut and pecan the part which splits open is called the husk or shuck;

it is probably a modified involucre. The nut has a hard stony pericarp; the seed coat is very thin, like that in the walnut.

The Acorn.—The fruit of the oak (Quercus) is a nut resting in a cup (Fig. 461). The cup is a sort of involucre consisting of a number of bracts grown together.

The Fig.—The fig is a hollow, succulent, pear-shaped axis containing the numerous achenes within. The hollow axis which becomes the fig is a kind of inflorescence (Fig. 489).

Seedless Fruits, Parthenocarpy.—Many fruits like the commercial banana, Washington navel, or seedless oranges bear no seeds. The expression, "blind fruit" is applied to those fruits in which the pistil develops into the normally appearing fruit but without seeds. Frequently fruits of the maple (Acer) will so develop. The phenomenon is known as *parthenocarpy*. A satisfactory explanation is lacking. The seedless orange in all probability arose as a bud sport. Seedless fruits doubtless originated in nature and without the aid of man.

Summary of Angiosperms.—The flowers of Angiosperms are not borne in cones. The parts are arranged spirally or in circles (cyclic). The flowers are either staminate or pistillate (diclinous) or they may be composed of both stamens and pistils (monoclinous). Progressive evolution in the flower consists, (1) in the union of the parts of the same cycle; (2) in the gradual union of the different cycles; and (3) in the complete union of all parts together with a reduction in the number of parts and the high specialization of the parts remaining, as in the orchids and composites.

The carpel or carpels form closed cavities containing the ovules and later the seeds.

Pollination consists in the transferral of pollen from stamen to stigma. The agencies of pollination are wind, water, insects, birds, and the flowers themselves. The most varied and wonderful adjustments or adaptations may exist between the flowers and the pollinizing agencies. The pollen tube grows from stigma into the ovule. As in the Gymnosperms it bears two sperm nuclei.

The megagametophyte (embryo-sac) consists of seven cells, the two most important being the *egg* and the *endosperm* cell. There is but one endosperm cell present before fecundation. In fecundation, one sperm nucleus unites with the egg nucleus, the other sperm nucleus being absorbed as food. In some plants the second sperm nucleus unites with the two polar nuclei in the endosperm cell to form the nucleus of the endosperm cell.

After fecundation, the zygote (fecundated egg) develops into the embryo sporophyte, and the endosperm cell into the endosperm. Endo-

sperm is developed in every seed. One of two conditions is the final result: (1) if the embryo grows so fast that the endosperm is all consumed by the time the seed is mature, the seed has a large embryo and no endosperm (bean, peas, peanut, etc.); (2) if the embryo grows more slowly than the endosperm, the seed will reach maturity with a small embryo and a large endosperm (castor oil seed, Indian corn, wheat, lily, coconut).

Fruits are of many kinds and manifold in character.

Dispersal of fruits is accomplished by wind, water, animals, including man, and by devices developed by the plants as adaptations for dispersal. Many are the adaptations between seeds and fruits and the dispersing agency.

TOPICS FOR REVIEW AND DISCUSSION

How does the carpel of an Angiosperm flower differ from that of a Gymnosperm flower?

What are the essential parts of a flower? What are the accessory parts?

Where are the megaspores developed?

What part of the ovule is homologous with a megasporangium of the Pteridophyta?

How many microsporangia are represented in a typical anther?

At what step in the life cycle of an Angiosperm does the reduction in the number of chromosomes take place?

Name the two gametophytes in Angiosperms. How many cells make up each in typical cases?

What two parasitic structures develop inside the ovule following fecundation?

Upon what is each parasitic?

Explain how it happens that certain seeds contain endosperm when mature, while others do not. Give an illustration of each kind of seed.

What is Xenia? What is regarded as the cytological basis of Xenia?

What happens to the second sperm nucleus in Lilum while the first unites with the egg nucleus?

Why is a flower regarded as a modified stem or shoot?

What kinds of flowers are held to be more primitive?

What family of monocots has the most highly specialized flowers? What families of the dicots have the most highly specialized flowers?

Write a diagram of the life cycle of an Angiosperm and indicate the haploid and diploid structures by the symbols x and $2x$ respectively.

In the progressive evolution of flowers from the simpler to the more complex, what has happened to the members belonging to the same cycle or cycles? What has happened to the different cycles?

Does the union of parts indicate progressive evolution in flowers?

In the evolution of the flower from Ranunculus to the Compositae has there been an increase or reduction in the number of parts?

What in the dandelion flower is homologous with the calyx?

What is self pollination? Cross pollination?

What are the agencies of cross pollination?

Are cleistogamous flowers cross pollinized in nature? Why?

What is protandry? Protogyny?

In monoecious and dioecious plants why are there more staminate than pistillate flowers?

Which plants produce the greatest quantity of pollen, those which are pollinized by insects or by the wind?

What plants have light, dry pollen?

What are nectaries? Are nectaries ever produced upon parts of the plant other than flowers?

What enables insects to find flowers?

What color have flowers which are pollinized by night flying insects?

Are there more yellow flowers in the spring than in midsummer?

What kinds of insects are the more frequent visitors of blue and red flowers?

What bees are most successful in pollinizing red clover?

Why do insects visit flowers?

How do bees make honey?

What is "bee bread"?

How is the jack-in-the-pulpit pollinized?

What is meant by the expression "unbidden guests" as applied to flowers?

Name two plants each of whose flowers are pollinized by one species of insect and *only* one?

What are dehiscent fruits? Indehiscent fruits?

What kinds of fruits in the strict botanical sense are the following: apple, pear, plum, grape, tomato, banana, orange, bean, cucumber, water melon, pineapple?

Botanically speaking what is the real fruit of the strawberry?

Why is the strawberry referred to as an accessory fruit?

From what part of the flower in the strawberry is the pulp derived?

What fruits are sold in the market as vegetables?

What is a fig in the botanical sense?

How can you distinguish the fruit of the raspberry from that of the blackberry?

Distinguish between a racemose inflorescence and a cymose inflorescence.

Who was Charles Darwin? Upon what botanical subjects did he write?

What are "caprifigs"?

What is the caprification of the fig?

What part of the flower gives rise to the fruit in Angiosperms?

What are diclinous flowers? Monoclinous flowers?

In the case of diclinous flowers which one gives rise to seed and fruit?

What is parthenocarpy? Give several illustrations.

What is apogamy in Angiosperms? Name an apogamous angiosperm.

Distinguish monocotylous plants from dicotylous plants.

What evidence can you give to support the view that the dicots are more primitive than the monocots?

Who was Asa Gray? By what work is he most widely known?

CHAPTER XX

DISPERSAL OF SEEDS AND FRUITS

Seeds are devices for the reproduction and dispersal of plants. In the distribution of seeds and fruits, there are many adjustments or adaptations between the seed or fruit and the natural agencies or forces of the environment. The natural agencies are water, wind, and animals. In a large number of plants there are present various structures which accomplish self dispersal.

FIG. 495.—Fruits with elastic valves for slinging seeds, the "sling" fruits. A, wild geranium (*Geranium palustre*) with persisting calyx. The five carpels surrounding the elongated torus, break first at the bottom, then curl up suddenly and sling the seeds out of the basal parts which have opened along the inner sides. B, fruit of touch-me-not (*Impatiens noli tangere*). The carpels (right) curl up elastically from the base and throw out the seeds. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

Self Dispersal.—After the seeds are ripe in certain plants, the parts of the fruit, whether sappy or dry, separate and bend or roll up suddenly in such a manner as to throw the seeds some distance from the parent plant.

As an illustration of fruits with dry elastic parts, may be mentioned those of the wild geranium. Here the five carpels which surround the elongated torus break first at the bottom, and, curling up suddenly, they sling the seeds out of the basal part which opens along the inner side (Fig. 495, A). As the carpels dry out they shorten on one side until the

strain breaks them apart, when they suddenly become elastically curled. Such fruits are sometimes called "sling" fruits or "catapult" fruits. Other illustrations are found in the violets, various legumes, such as vetches and some beans, in the witch hazel (*Hamamelis virginiana*) and in the castor oil plant, or castor bean (*Ricinus communis*).

In the violet (Fig. 496) the pod opens into three boat-shaped parts, each containing a number of smooth, ivory-white seeds. As the keel-shaped parts dry out, the sides press harder and harder upon the seeds until they are suddenly shot out to a distance much as one may shoot

FIG. 496.—Fruit of violet forcibly ejecting seeds. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

FIG. 497.—Fruits of *Lathyrus vernus*. The legume at the left has burst and thrown out the seeds. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

a smooth bean or marble from between the pressed thumb and finger. The mature and drying pods of some vetches and beans open with an elastic twist by which the seeds are tossed out (Fig. 497). The fruit of the witch-hazel hurls its seeds forth in a similar manner. In a dry room the fruits often open with a loud pop (Fig. 498). In the popping varieties of the castor oil plant the seeds may be shot a distance of four or more meters.

Among plants with sappy fruits are the touch-me-nots and the squirting cucumber. In Fig. 495, B we have an unopened and an open fruit of the touch-me-not (Impatiens). Here the five carpels separate when mature and curl up, suddenly tossing out the seeds. The cells on the

outside being more turgid than those on the inside, cause the outer side to elongate, producing a sudden inward curling as shown in the figure. If the ripe unopened pods be given a slight pinch or shock, the process may be readily observed. Species of the sour clover (Oxalis) scatter their seeds in a similar manner. In the squirting cucumber, the rind of the ripe fruit is so distended by the very sappy pulp surrounding the seeds that it contracts and ejects the mass through the opening made when the fruit separates from its pedicel (Fig. 499).

Dispersal by Water.—Fruits and seeds which float in water may be carried long distances by currents of the ocean and rivers. This is not

FIG. 498. FIG. 499. FIG. 500.

FIG. 498.—Fruit of witch hazel (*Hamamelis virginiana*) discharging its seeds. (From Beal's "Seed Dispersal," Ginn & Co.)

FIG. 499.—The squirting cucumber (*Ecballium elaterium*). (From Jenkins.)

FIG. 500.—Seed of water lily (*Castalia odorata*), with air holding cover (aril).

only true of seeds but of twigs and off-shoots as well. Some seeds possess a loose, air-holding aril as in the white water lily (Fig. 500); others, as in some Sedges, have loose-textured carpels, which form very efficient floats. The fruit of the Lotus (Nelumbium) consists of a large, light, top-shaped structure with the acorn-shaped seeds embedded in the upper surface (Fig. 501). It floats upon the water like a keeled boat, and may be blown long distances. From time to time, it is said seeds are dropped when the fruit is toppled about by the waves. In time the whole becomes water-logged and sinks to the bottom.

One of the most frequently cited cases of wide dispersal by water is that of the coconut on account of the thick, fibrous husk which enables

the fruit to remain afloat for a long time (Fig. 502). It has been reported, however, that the viability of the coconut is destroyed after lying in sea water a few days. Seeds of certain strand plants may remain in sea water for a long time and retain viability. Those of the strand plant, *Suriana maritima*, have been shown to be viable after lying in sea water for a period of four months.

It should be remembered also that swift-flowing water will carry along nuts and other heavy fruits which sink ordinarily in quiet water. Fruits and seeds which are especially adapted to wind dispersal may be scattered by water also.

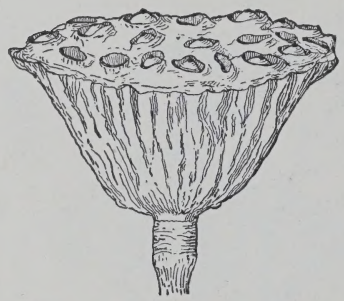


FIG. 501.—Top-shaped fruit of the lotus (Nelumbium) adapted for floating. × ½.

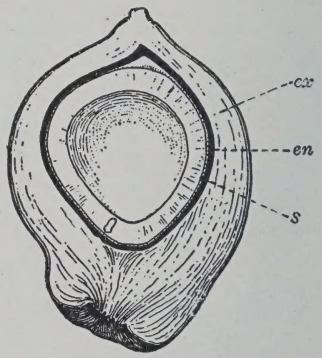


FIG. 502.—A coconut halved lengthwise, reduced. There is shown the air-holding fibrous husk (*ex*), the hard shell (*s*), the "meat," endosperm (*en*) and the central cavity containing the sap, "milk." Below in the endosperm may be seen the small embryo which lies just under the open eye. (From Le Maout and Decaisne.)

Dispersal by Currents of Air.—Doubtless the commonest and most efficient means of dispersal is the wind. Fruits and seeds are often provided with wide spreading and light outgrowths which may take the form of "wings" or "down." These outgrowths may act after the manner of a sail or like a parachute or both. The following will serve to illustrate the character of seed or fruit and the principle involved.

Very familiar cases are the dandelion, thistle, milkweed, cotton, willows and willow-poplars. The heads of mature fruits of the dandelion expand into the familiar "blow balls" (Fig. 503, A). Each fruit is an achene prolonged into a long slender beak, bearing a tuft of white capillary pappus (Fig. 503, B, C). This pappus spreads out like the rays of an umbrella and functions in the manner of a parachute. The seed of the

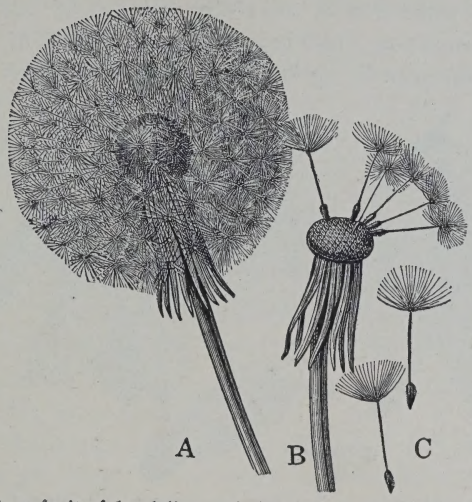


FIG. 503.—Mature fruit of dandelion. A, head of fruit or "blow ball." B, several fruits, showing attachment to the receptacle. C, two separate achenes, each with a tuft of hairs. (From Kerner's "General System of Botany," Firmin—Didot & Co., Paris.)

FIG. 504.—A fruit, "boll," of Barbadose (Sea-island) cotton, open, exposing the numerous hairs (commercial cotton) which are outgrowths of the seed coats. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

common milkweed (Asclepias) bears a terminal tuft of long silky hairs near the hilum, while that of the cotton plant (Fig. 504) is covered all over with numerous long white hairs (commercial cotton). In the willow the down-like out-growths spring from the seeds; in the Compositae, it

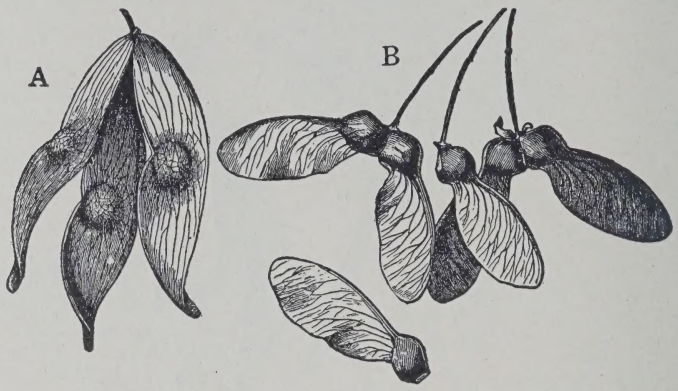


FIG. 505.—Winged fruits. A, "tree of heaven" (*Ailanthus glandulosus*), each carpel with a double wing. B, fruit of the maple tree (*Acer saccharum*), each carpel with a single wing. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

is the modified calyx; in the Clematis, the persistent style; and in the "smoke tree" (*Rhus cotinus*) it is the aborted flower stalks.

The fruits mentioned are small and light, being borne, with the exception of the willows and poplars, upon low herbs or shrubs. In the case of tall plants the fruits or seeds, as a rule, are larger and heavier. They are provided with relatively broad wings, as in the maple, "tree of heaven" (Ailanthus), elm, the "hop tree" (Ptelea) and in the linden or basswood (Tilia) (Figs. 505 to 508). The wing in the maple, tree of heaven, hop tree, and elm, are outgrowths of the ovulary, while in such plants as Bignonia (Fig. 507) and Catalpa, it is a part of the seed. The wing in the linden is a leaf-like outgrowth of the peduncle (Fig. 508).

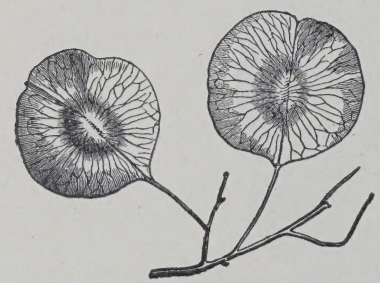


FIG. 506.—Winged fruits of Ptelea. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

The term "tumbleweed" is applied to the dead and dried part of certain plants which are broken off at the ground, and rolled or tumbled about by the wind, dropping their seeds along the way. As they mature and dry out, twigs and branches curve inwardly forming a sort of ball or rounded structure. In level localities tumbleweeds often accumulate in

windrows along such barriers as fences, ditches, and hedges. Some common tumbleweeds are the pigweed (*Amaranthus graecizans*), the

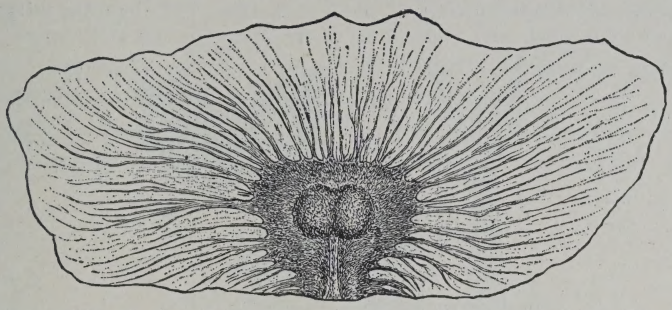


FIG. 507.—Winged seed of *Bignonia mucronata*. (Strasburger, Macmillan Co.)

Russian thistle (*Salsola tenuifolia*), pepper grass (Lepidium) and old-witch or tumble grass (*Panicum capillare*).

Dispersal by Animals.—Animals are important and effective agents in the scattering of seeds. Seeds which are dispersed by animals are

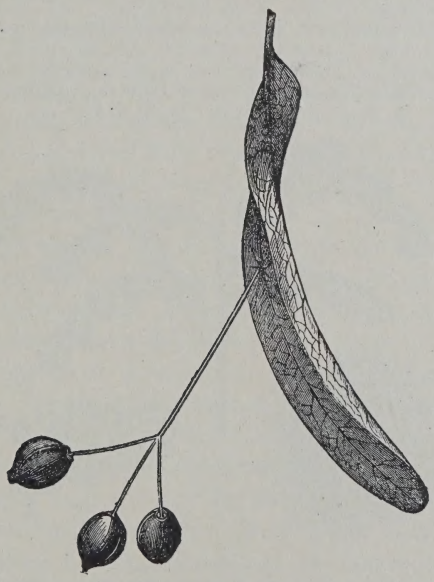


FIG. 508.—Fruit of the linden (Tilia). The wing is an outgrowth of the peduncle. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

contained either in fruits provided with hooks or spines, or which are pulpy and palatable to the animals that seek such fruits as food.

Of those which possess hook-like appendages, the Spanish needles, cocklebur, tick trefoil, and burdock are common examples. The hooks

enable the fruits to adhere to the coats of animals and to the clothing of man (Figs. 509, 510). Such hooks have diverse origins. In the burdock they are the developed bracts of the flower head, but they are outgrowths

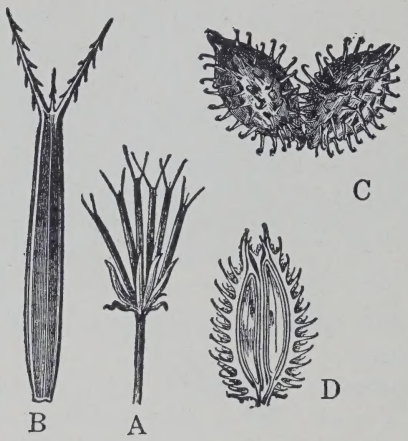


FIG. 509.—Fruits provided with hooks and barbels. A, cluster of fruits of the Spanish needle (*Bidens bipinnata*). B, a single fruit enlarged, showing (barbed awns, representing the calyx lobes by which it adheres to animals and to the clothing of man. C, two fruits of the cockel-bur, (*Xanthium*) showing hooked appendages of the involucre. D, a fruit of the same halved, showing two seeds, the upper usually germinates a year later than the lower. (A, B, C, after Kerner; D, after Arthur.)

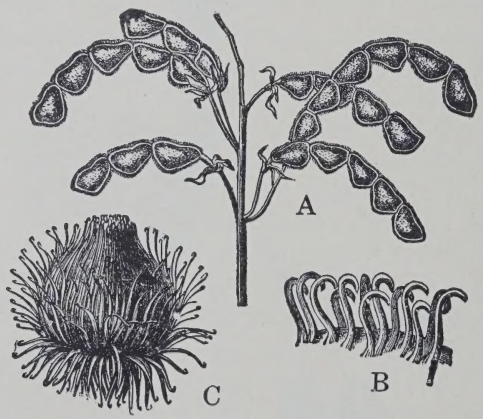


FIG. 510.—Fruits provided with hooked appendages. A, the tick trefoil, "beggar's ticks" (*Desmodium canadense*); the pods separate in sections, each containing one seed. B, some of the stiff hooked hairs enlarged, which clothe the surface of the parts. C, head of burdock (*Arctium lappa*). (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

from the ovulary in the cocklebur and tick trefoil; in the Spanish needle the barbed appendages represent the modified calyx. The hooks are of gigantic size in the unicorn-plant (Martynia).

The fruit of the mistletoe is in some respects intermediate between those which adhere to the surface and those which are eaten. The sticky pulp of the fruit adheres to the feet of perching birds and to the beaks of those which attempt to use the fruit as food. The seeds adhering to the feet, are eventually brushed off by contact with the bark of trees, while those sticking to the bill are wiped off by the bird.

It may be mentioned here also that many kinds of seeds are carried in mud adhering to the feet of wading birds and to those of certain domestic animals.

FIG. 511.—Ant ready to take the seed of bloodroot (*Sanguinaria canadensis*) which is provided with a sappy crest, caruncle. (From Beal's, "Seed Dispersal," Ginn & Co.)

Fleshy fruits with their variously colored, edible, and palatable pulp are easily found and eagerly eaten by birds and other animals. In many cases the seeds of such fruits are protected against injury from the digestive fluids so that they will germinate on being eliminated from the alimentary tract.

The hard protective covering of the seed is derived either from the seed coat or from the wall of the ovulary. The stony pit of the peach, plum, cherry, etc. is derived from the wall of the ovulary.

Many seeds are brightly colored and without any pulp, as in the Magnolia and in certain Leguminosae.

Seeds provided with an aril, as in the twin leaf (*Jeffersonia diphylla*), the Celandine poppy (*Stylophorum diphyllum*), the bloodroot (*Sanguinaria canadensis*) and in others, are carried underground by ants which not only scatter the seeds but plant them as well (Fig. 511).

Lastly, the habits of squirrels and other food-storing animals are worthy of note. Squirrels hide walnuts, hickory nuts, etc., in the soil for use during the winter months. Many nuts thus secreted are not found by the animals, and they readily germinate and grow. Along fence rows are often seen such trees as the walnut, hickory, wild black cherry, the red cedar and hackberry, which have grown from seeds dropped by squirrels and birds.

Dispersal by Man.—If great distances and wide barriers, such as oceans, broad deserts, and great mountain ranges, are taken into consideration, man is probably the most efficient agency in the dispersal of plant life of all kinds. When the human race first began cultivating and carrying economic plants from place to place, no one knows. When settlers came to America from Europe they brought with them seeds of

their favorite grains, vegetables and garden flowers. Similar practices have been going on for ages, but never more extensively than at the present time. The governments of the more enlightened and progressive nations have their skilled agricultural explorers searching in all parts of the earth for new plants which may prove useful or ornamental in particular localities in the home lands.

Through channels of trade man has accidentally, unknowingly, carelessly, or unwittingly brought into his own country from abroad many plants which have come to be extremely destructive as parasites or very troublesome as weeds. It often happens that the foreign plant will thrive better in its adopted country than certain native species, thereby crowding out the latter. As an illustration may be mentioned the common ragweed (*Ambrosia artemisiifolia*). A certain per cent. of weed seeds are almost always present in commercial seeds. It is said that the Russian thistle was first introduced into South Dakota in flaxseed brought from Russia in 1873 or 1874. Since that time it has become a common weed in a large area of the United States. One needs but to walk along a railroad in the country to find always a few plants which are not native to the locality. The invaders came from seeds which fell from cars in which feed and live stock were transported. It is readily understood that a thistle or a dandelion seed which lodged against a freight car or a passenger coach in Minnesota might be dropped in Tennessee or Louisiana.

Not only does America suffer from the invasion of noxious weeds from other countries, but, on the other hand, American plants have in some cases overrun other countries. The small aquatic plant, Elodea, which is so extensively used in laboratory studies, is troublesome in Great Britain, and in Germany it is referred to as the American water pest. Species of the prickly pear cactus (Opuntia) and of the century plant, which are native to North America, are conspicuous in certain localities of southern Italy and in other lands.

The various agencies above cited often work together in dispersal. In hilly or mountainous regions nuts will, under the force of gravity, roll into gullies whence they are carried by water to lower levels.

TOPICS FOR REVIEW AND DISCUSSION

In what general class of fruits are the seeds alone dispersed?

In what kinds are the fruits scattered along with the seeds?

Which method of dispersal, do you think is more advantageous to the plant, self dispersal or dispersal by environic agencies?

What are "sling" fruits? "Catapult" fruits?

Explain the method of dispersal in the squirting cucumber.

Explain the method in the violet and in Oxalis.

Why was the touch-me-not so named?

Mention correlations between seeds and fruits and water as the dispersing agent.

As a rule, are seeds or fruits adapted to wind dispersal produced by tall plants or by low plants?

Does the wing of a seed function the same as the wing of a bird?

By what natural agency do you think seeds are carried the greatest distances?

What are tumble weeds?

Why are walnut and wild cherry trees so often found along a fence row?

Name some plants which plant their own seeds.

What animals plant seeds?

Does the plant profit by having hooks and barbs developed upon seed or fruit?

What is the correlation between the pulp of the cherry and seed dispersal?

Is the stony cover about the seeds of cherries of any value to the species?

Is it advantageous to the species that cherries and plums are green when young rather than conspicuously colored?

What scatters the seeds of the mistletoe?

What kinds of fruits are injurious to the animals by which those fruits are scattered?

Why are many plants which are not native to the locality found along railroad tracks?

In what way do the dog and cat scatter seeds like those of the plantain and pig weed (Amaranth)?

Discuss man as a seed dispersing agent.

What are the principal natural agencies in the dispersal of spores of lower plants?

Why are there more parasitic plants and animals in this country than there were one hundred years ago?

Name some plants in which the turgidity of tissues play a role in dispersal.

What are viviparous seeds?

Do you know any plants which possess viviparous seeds?

Who made studies in regard to the number and character of seeds carried on the feet of wading ard swiming birds?

Upon what part of the plant is commercial cotton developed? Is the cotton of any value to the plant?

CHAPTER XXI

GEOGRAPHIC DISTRIBUTION OF PLANTS

I. REGIONAL DISTRIBUTION

Taking into consideration the distribution of plant life over the entire land surface of the earth, one finds that certain types of vegetation are characteristic of areas of great extent, such as forest regions, deserts, grasslands (prairies, steppes) and tundras. The dominant and characteristic form of vegetation covering these several regions, is determined largely by temperature and rainfall. The factors are, therefore, climatic

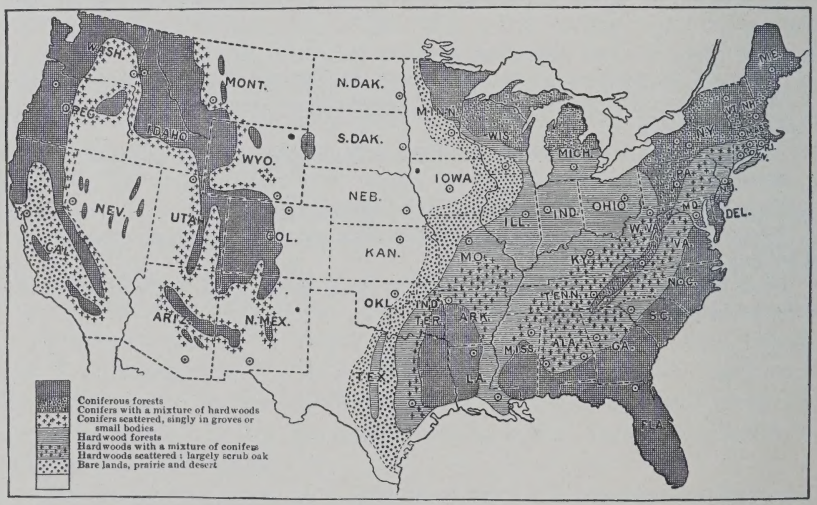


FIG. 512.—Map of the forest regions of the United States. (After Roth.)

factors. The plant geography of the United States and adjacent territory to the north and to the south will serve to illustrate the characteristics of certain of these great regions.

The Central and Eastern Forest Region.—The central and eastern forest region of the United States extends from near the western part of Minnesota and Iowa, the eastern part of Kansas, Oklahoma, and Texas to the Atlantic Ocean (Fig. 512). At the time the European settlers came, a magnificient forest of deciduous hardwoods and coniferous evergreens covered this area with the exceptions of the prairies of Indiana and Illinois and other limited grassy stretches and "openings." In the central

part of this region extending over a part of southern Michigan, southern Wisconsin, a large part of eastern Illinois, Indiana, Ohio, the larger part of Kentucky, and down the Mississippi River to New Orleans, the deciduous hardwoods such as the oaks, hickories, yellow poplar (tulip tree), beech, maples, elms, sycamore and others were the dominant trees. New England, New York, and the Appalachian mountains to the southward were covered with coniferous evergreens with a mixture of deciduous trees. This type of forest extended also to the north and east into Canada. Of the evergreens, the finest lumber tree was unquestionably the white pine (*Pinus strobus*), which was more abundant in the north and east. For a long time the greatest hardwood industry was centered in Indiana.

The eastern part of the area, comprising a strip along the Atlantic from Virginia to Florida, along the Gulf to the southern part of Texas and up the Mississippi, the lower Ohio and Wabash rivers contains important growths of the bald cypress. In the brackish marshes along the seaboard, the mangrove flourished.

The western edge of the central forest contained scattered hardwoods, mainly scrub oak, which soon merged westward into the drier grassland region of the great plains.

The Rocky Mountain Forest Region.—This area follows the great mountain range from central Arizona and northern New Mexico to Idaho, Montana and northward to Alaska. The region includes diverse formations, ranging from coniferous forests to mountain meadows. The characteristic lumber trees are the Douglas spruce (Pseudotsuga), the sugar pine and other pines along with true spruces (*Picea*).

Forest of the Pacific Slope.—This forest area lies chiefly west of the Cascade Range, extending in a narrower strip along the western slopes of the mountains in eastern California, but widening out in the northern part of the state and continuing northward into Oregon, Washington, and British Columbia. The climate of the Pacific slope is much milder than in the Rockies. The mountains are heavily timbered, especially the western slopes. The dense forests abound in such valuable coniferous trees as the western white pine (*Pinus monticola*) several species of fir (*Abies*) and the western hemlock (*Tsuga heterophylla*).

The southern portion of the Pacific slope south of the Oregon line is characterized by the evergreen conifers of California, the sugar pine, the yellow pine, and others. Here are found the great redwoods, *Sequoia sempervirens* and *Sequoia gigantea*, the latter being the greatest and most imposing of all trees.

[The forests of temperate regions of the Old World exist under conditions similar to those in North America. The tropical rain forests are jungles of many species of trees upon whose branches grow many epiphytic

plants. Among the trees of the dense forests are many gigantic vine-like plants (lianas) which clamber among the branches or lash themselves to the trunks by means of cord-like roots (See Fig. 147).]

Grasslands, Prairies (Grass Steppes).—The vast territory extending from the eastern forest region to the foot hills of the Rocky Mountains is known as the *great plains* or prairies (Fig. 512). Dry grasslands in Russia and Central Asia are known as *steppes;* in South America as *pampas* and *llanos*. Our western prairies are vast grassy "plains on whose horizon the curvature of the earth is made manifest." They are the result of a distinct inland climate with its long severe winters and hot and dry summers. The summers are often rainless in the western portion

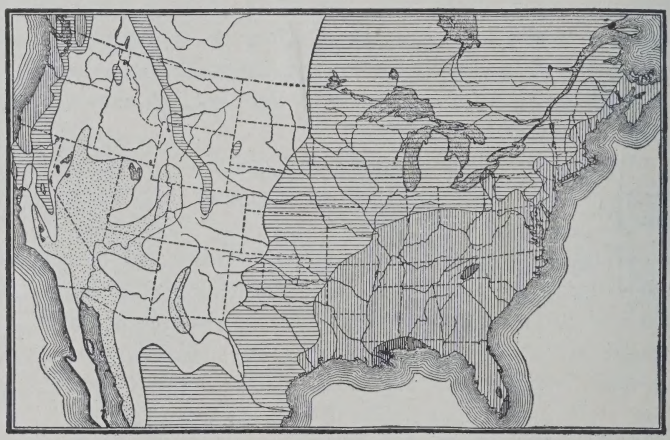


FIG. 513.—Annual rainfall in the United States. Darkest shaded areas, 80 inches and over; lighter vertical lines, 40 to 80 inches; horizontal lines, 20 to 40 inches; blank, 10 to 20 inches; dotted less than 10 inches. (After W. M. Davis.)

from midsummer onwards. Hot days may be followed by cold nights. The annual rainfall varies from 10 inches to 20 inches (Fig. 513). The most favorable vegetative season occurs in the spring (May) when rains are more frequent. The climatic conditions prevailing throughout the year prevent the growth of forests.

The prairies are clothed with grasses, other perennial herbs and some undershrubs. They are treeless or contain open tree-vegetation (Fig. 514). Differing from the grasslands of Russia, our prairies are crossed by great rivers along whose courses woodlands occur.

In the eastern portion of the great plains especially, conditions are more favorable for vegetation. Here various grass associations abound, such as prairie-grass, "buffalo-grass," etc., which afford excellent forage. Buffalo-grass land is clothed with a low velvet-like grassy carpet, green in the spring, but gray at other times. Several kinds of grasses make

up buffalo-grass, of which *Munroa squarrosa*, *Buchloe dactyloides*, and *Bouteloua* are the dominant ones. There are many others. Intermingled with the grasses are many Compositae, legumes and other herbs, which give to the landscape its characteristic appearance.

These prairies were the home of vast herds of bison and antelopes, which, however, have disappeared as the result of the greed, stupidity, and lack of foresight of "civilized" man.

FIG. 514.—Grass-steppe of the plain region. The dominant vegetation consists of coarse grasses, herbs, and low shrubs (sage brush). The cottonwood tree (Populus) in the foreground, and others showing dimly in the background indicate spots of greater moisture or a stream. (From Coulter's "Plant Relations," Courtesy of D. Appleton & Co.)

Grasslands in Other Parts of the World.—Vast grasslands, *grass steppes*, occur in South Russia, Hungary and Central Asia. As in other steppes, the character of the vegetation varies with the geographic situation and the richness of the soil. In the South-Russian steppe the soil, like our prairies, is black earth which supports forage grasses and some legumes. There are also *spring plants* with bulbs and tubers. In the Orenburg District there is a gay showing of Liliaceae (Fritillaria, Allium, Scilla, Tulipa, Iris, Corydalis and Adonis). Among the peculiar phenomena of this steppe are "rolling plants," which are represented by *Gypsophila paniculata* (Baby's Breath) and *Rapistrum perenne*. When these are

dead and dried out they are dislodged by the wind and become matted together, often into gigantic masses, which the storm drives bounding over the plains in great leaps, hence the popular name, "steppe-witch."

The Pampas of South America.—The pampas are another great grass steppe, level or somewhat undulating, and treeless. They occupy the vast rockless, alluvial plains that extend from the Atlantic coast to

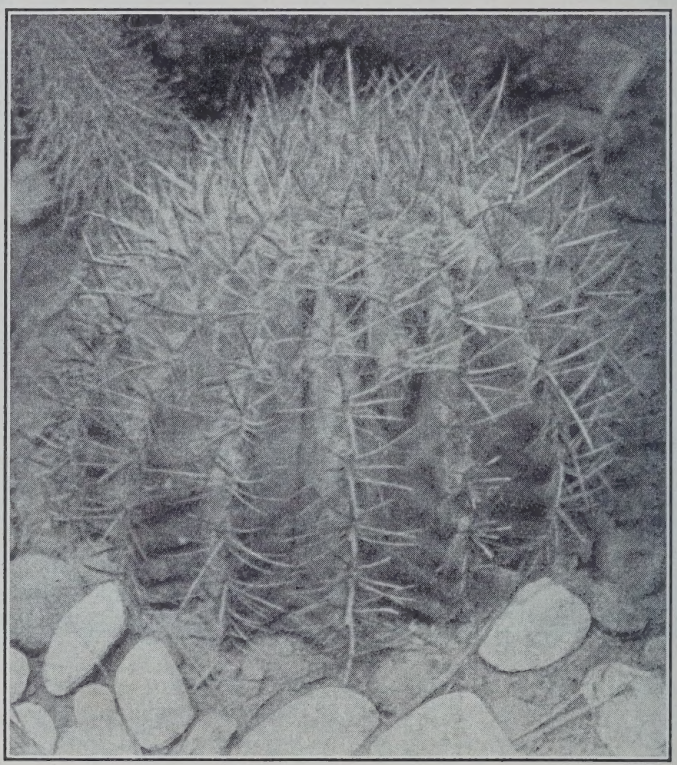


FIG. 515.—A globular cactus. Note the ribbed stem, the strong spines and the absence of leaves. (From Schimper's "Plant Geography," Clarendon Press.)

the Andes, and from Patagonia to the forest of Paraguay and Brazil. The boundless, level or undulating, treeless surface is clothed with perennial grasses and herbs like "a shoreless sea of grasses on whose horizon the eye finds no resting point, save where the sun rises and sinks."

The genera of grasses and herbs belong to many families which are widely distributed over the surface of the earth. It is interesting to note that numerous European species have succeeded in crowding out completely for miles the inland vegetation. These include not only such

thistle-like Compositae as Cynara, Silybum and burdock, also *Lolium perenne*, *Hordeum murinum* and *Medicago denticulata*, and others. It is said that three-fourths of the flora around Buenos Ayres consist of introduced species, largely from the Mediterranean countries.

Deserts and Shrub Steppes.—Grassland, shrub-steppe and desert correspond to *three stages of descreasing frequency in rainfall.* In the desert where rain falls at quite irregular times, and is continuously lacking for a long time during the season otherwise most favorable to plant life,

FIG. 516.—A cactus desert.—Note the rough, rocky soil with occasional clumps of globular forms of cactus. (From Schimper's "Plant Geography," Clarendon Press.)

only the scantiest vegetation can exist. Here and there are dotted low, greyish-green plants which stand wide apart, while the large intervening stretches of soil are devoid of vegetation. It is only when a shower moistens the soil that numerous annual herbs spring up from seed, bear fruit and die a few weeks later. Growth is rapid whenever suitable conditions return. After a rain in the spring, green shoots suddenly appear upon the parched shrubs, and a profusion of beautiful flowers bursts forth.

Deserts vary greatly both in the character of the soil and in the quantity of rainfall. On the desert of Atacama in South America it is said that rain scarcely ever falls. At Walfish Bay on the coast of South Africa the mean annual rainfall, which descends on only six days in the year, is seven millimeters. In most deserts there are more favored localities in which the rainfall is greater, but too frequently the larger quantity of water which falls during storms runs off in torrents in the previously dry river beds.

The soil is far from being uniform. There are regions of pure sand which is shifted by the wind into ever changing dunes. In some deserts,

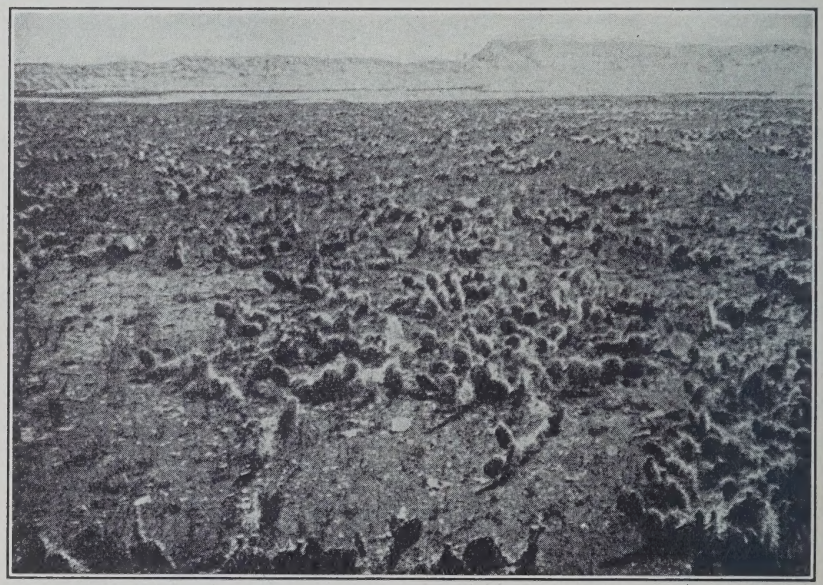


FIG. 517.—A cactus plain covered with the prickly-pear cactus (Opuntia). A bit of the "Big Bad Lands" of South Dakota. Sheep Mountain in the background. (From Schimper's "Plant Geography," Clarendon Press.)

such as parts of North Africa the surface is solid rock. In others it is gravelly and stony; and in still others, such as the deserts of the Mexican plateaus, the soil consists of firm, reddish clay, rich in stones. In the dry season the clay becomes as hard as rock and cracks into numerous fissures.

The plants are small, scrubby, and often without leaves, or these and branches may be developed as sharp spines which are frequently hooked (Fig. 515). The thick and often curiously shaped stems are sometimes succulent, containing much mucilage in pith and bark. The epidermis is thick and covered with a thick layer of cutin; the stomata are deeply

set. In short, the plants are so developed as to be able to conserve their moisture to a high degree (Figs. 515, 516, 517).

The great deserts are the Sahara, the Egypto-Arabian Desert, the Desert of Gobi in Mongolia, the deserts of South Africa, and the arid regions of the southwestern portion of the United States, such as the Mohave Desert, the Ralston Desert, the Colorado Desert in southern California, and the arid Mexican plateaus.

The Arid Regions of the United States.—In the dry regions of the southwestern United States and northern Mexico, the localities differ geographically as well as in the character of their vegetation.

In the dry and barren land between the Rocky Mountains and Sierra Nevada, the vegetation consists of shrubs and undershrubs intermingled with herbs. The dominant plants are species of Artemisia, woody Compositae, and Chenopodiaceae. Trees are absent, and there is no carpet of grasses, but in its place are a few species of small shrubby plants which crowd out all other vegetation. Uniformly gray or olive-tinted shrubs are characteristic of the vast area. Many of the plants are clothed with colorless epidermal hairs which impart the grayish or silvery appearance. The most abundant is the "sage-brush" (*Artemisia tridentata*), an undershrub that extends over areas so vast that the unaided eye can see nothing beyond. It rarely exceeds one meter in height, and never grows so densely as to bar the way. The region, or a part of it at least, is more on the order of a shrub-steppe, for, as stated by Watson, there is not a spot devoid of vegetation, even in the driest season. The shrubby vegetation of our South West is commonly known as *chapparal.*

Bushland occurs in Arizona, New Mexico, Texas and northern Mexico. According to Bray, two types of *chapparal* are to be found in Texas, which owe their differences to climatic and physiographic conditions. The chapparal in Texas is largely made up of species of Prosopsis, of red-bud (Cercis) and other leguminous plants, Prunus, stunted walnut (*Juglans nana*), mulberry, prickly ash, and others.

In addition to chapparal there are distributed throughout this region including the deserts in southern California (Mohave, Douglas, Ralston and Colorado deserts) many large and conspicuous succulent plants. Chief among those which make up this succulent-steppe are the tree-like yucca (Fig. 518), Agava and especially many of the Cactaceae. Here the giant cactus, *Cereus giganteus* (Fig. 519) "raises its mighty candelabra-like branches up to a height of some 18 meters, and covers the hills to such an extent that at a distance these seem to bristle with "needles."

Savannahs or Semi-Deserts.—In various regions of the dry tropics of South America and Africa are semi-deserts or thorny savannas. In

the caatingas (Caa-Tinga) the stunted trees often have curiously twisted, barrel or bottle-shaped trunks which branch sparingly at the top (Fig. 520). The leaves are small, leathery and often spiny. The trees protect

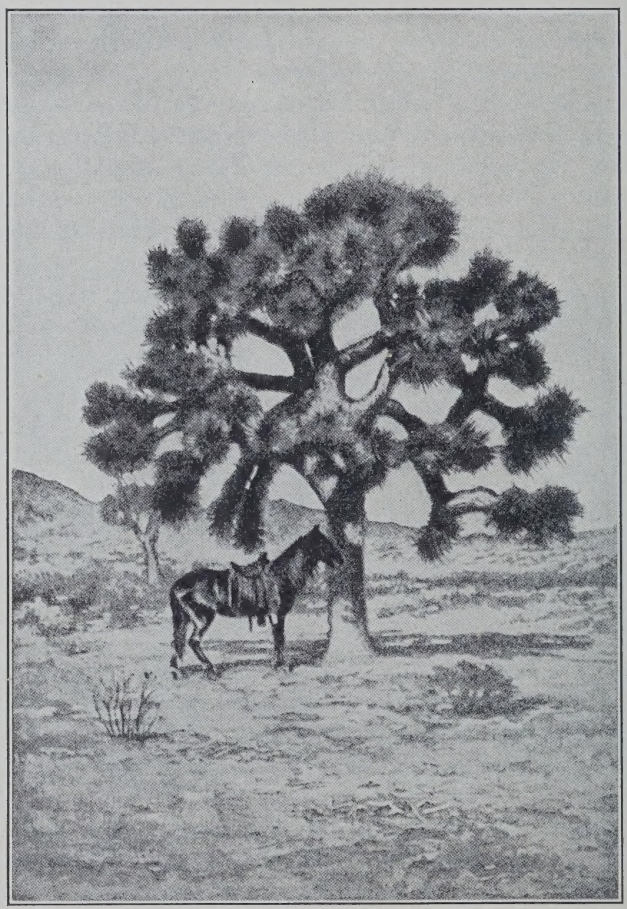


FIG. 518.—A magnificent tree yucca in the Mohave Desert. (From a photograph by Coville in Bergen & Caldwell's "Textbook of Botany," Ginn & Co.)

themselves by shedding their leaves wholly or in part during the dry season.

Cold Soil Regions, Tundras.—Tundras are cold, mossy, and, for the most part, treeless plains in the vicinity of the Arctic Circle. Extensive tundras occur in Northern Russia, Siberia and in the northern parts of North America.

The surface of the ground is covered by a dense growth of mosses and Lichens. In some places moss (Polytrichum) dominates (moss tundra); in others Lichens (*Cladonia rangiferina*, Reindeer moss) constitute the principal ground cover. In the Lichen tundra other species such as Iceland moss (*Cetraria islandica*) occur. During the Arctic summer the ground thaws to a depth of a few inches, or sufficiently to enable these hardy plants to awaken into activity and make new growths. In many locations, therefore, the shallow layer of soil with its carpet of vegetation rests upon a perennial bed of frozen soil.

In the tundras of Greenland stunted bushes (willow and birch) occur in certain parts. Tundras in Alaska and in the Old World afford excellent grazing for such animals as the reindeer.

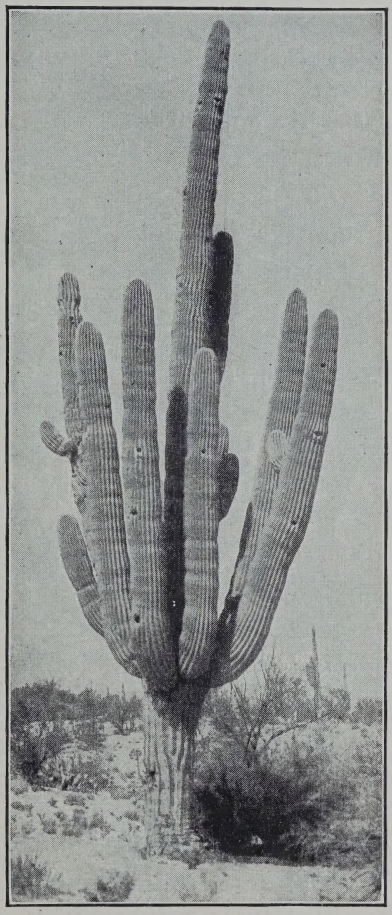


FIG. 519.—Giant cactus (*Cereus giganteus*) growing upon the rocky soil of the desert. Note the fluted trunks and thick branches. Grasses and low shrubby plants grow intermingled. (Gager.)

II. Topographic Distribution, Ecological Communities

In the preceding paragraphs attention was centered upon vegetation as characteristic of great areas. In certain of these great regions, especially where there is a more abundant rainfall, there occur smaller areas occupied by plants, which are similar in habit because of the place in which they live, i.e., their habitats. Plants which occupy the same habitat may be widely separated in relationship, for relationship is a matter of heredity. Habit is concerned chiefly with the vegetative organs,—leaves, stems, and roots. The factors which determine the habitat are topographic rather than climatic. Plants with similar habits and which occupy the same habitat constitute ecological groups or communities. The great groups are *Hydrophytes*, *Xerophytes*, *Mesophytes* and *Halophytes*.

Hydrophytes.—Hydrophytes are plants which live in relation to the *maximum* water supply. Their habitats are bodies of water and marshy or undrained soil. There are consequently two classes, *acquatic* plants and *marsh* plants, the latter being referred to as *helophytes*.

Aquatic Plants.—These grow entirely submerged, or they may float on the surface of the water. In those like the white water lily (*Castalia odorata*), all of the plant body is submerged with the exception of the leaf blades which lie flat upon the surface of the water. Among the submerged aquatics may be mentioned Elodea, eel grass (Fig. 521) (Val-

FIG. 520.—Tropical thorn-woodland, Brazil. (After Martins.)

lisneria), certain species of the bladderwort (Utricularia) (Fig. 72) and various pond weeds. Here belong aquatic algae and seaweeds, green, red, and brown. Submerged aquatics may be rooted in the mud or attached to some object in the water.

There is, however, a certain type of vegetation belonging to the Spermatophyta, Pteridophyta, and mosses which is not attached but free-swimming. Some float submerged like Ceratophyllum, species of Utricularia and the duckweed *Lemna trisulca*, while other species of Lemna, Wolffia, the water hyacinth (*Eichornia crassipes*), and the two water ferns, Azolla and Salvinia, float upon the surface by means of shoots or leaves. A few like *Hottonia palustris*, and *Jussiaea repens* (Fig. 149) are transitional between the rooted and the floating type.

FIG. 521.—Eel grass (Vallisneria). The plant grows under water rooted in the mud. The pistillate flowers are carried to the surface on long stalks which may be coiled to allow for variable depths of water. The staminate flowers which are borne beneath the surface break away when mature and rise to the surface where pollination takes place (see also Fig. 483). (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

Most aquatics are perennial. Salvinia and many algae are annual. Some hibernate during the winter. Bud-like winter shoots are developed upon such plants as Hydrocharis and Utricularia, which sink to the bottom in the autumn where they remain until spring when they rise to the surface and grow into adult plants.

Aquatic plants reveal many striking structural adaptations in both form and in internal anatomy. The epidermis is thin-walled, roots are greatly reduced or wanting, and the conducting and mechanical tissues are poorly developed. Another outstanding characteristic is the presence of many air cavities in all organs. In the water hyacinth, for example, the petioles of the leaves are greatly expanded and serve as efficient floats.

The tiny duckweed, Wolffia, the smallest flowering plant, consisting of a rounded body no larger than a medium pin head, is without differentiation into root, stem, and leaf. *Ceratophyllum*, *Utricularia vulgaris* and the water fern Salvinia are entirely rootless. Certain leaves of Salvinia are modified into structures resembling roots, which grow down into the water and function somewhat as balancers. In the duckweed, (Lemna), in Hydrocharis, Pontederia, and the water fern Azolla, roots may not branch and soon cease to grow. Root hairs are likewise absent in certain aquatic and marsh plants.

Plankton.—The term plankton is applied to the minute organisms, both plant and animal, which live near the surface of the water. Phytoplankton is composed of microscopic plants such as diatoms, blue-green algae, the one-celled plants, Peridineae, and others. In the sea, the quantity of plankton is very great. Diatoms, for example, are so numerous at times that they give the water a milky appearance. The plant life which makes up plankton constitutes the necessary food for small animals which in turn become prey for larger animals. Without plankton and other small vegetation large aquatic animal life could not exist.

Vegetation on Ice and Snow, Cryoplankton.—It has long been known that certain small plants and animals live on the snow fields and glacial ice in arctic regions and on high mountains, as the Alps, Pyrenees, and Andes. The plant life consists chiefly of green and blue-green algae, which, according to color produced upon the snow, are spoken of as *red snow*, *brown snow*, and *green snow*.

Red snow is probably the commonest and best known. It is caused by the presence of the blood-red unicellular alga *Haematococcus nivalis* (Chlamydomonas) and the blue-green, *Gloeocapsa sanguinea*, and others including a few diatoms. The tint varies from blood-red to rosy red and from brick-red to purple brown.

Brown snow owes its color also to various algae including a species of desmid with violet cell sap, together with Protococcus, diatoms and blue-

greens. These plants, when mixed with finely divided mineral particles have an important action on the ice in the interior of Greenland, as they absorb the sun's rays more strongly than ice, thus melting cavities in the latter.

Green snow is a phenomenon similar to the preceding. It is due to the presence of desmids, moss protonemata, Haematococcus and other algae. The tints are generally yellow or greenish yellow.

During the greater part of the year all of these plants are frozen in the ice or snow. When the sun melts the ice the dormant cells awaken into activity, grow and multiply in water whose temperature scarcely exceeds

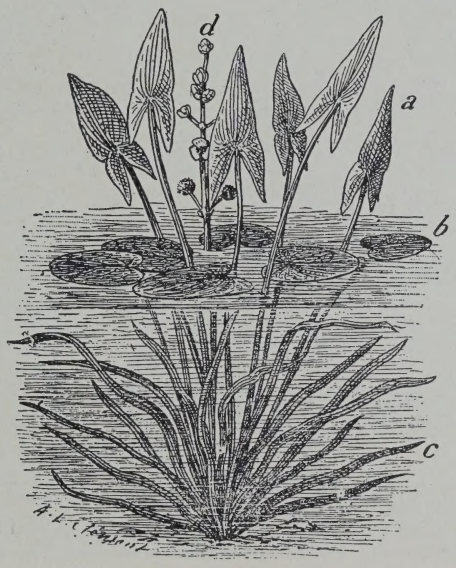


FIG. 522.—Leaf variation in an aquatic plant, *Sagittaria sagittifolia*. *a*, aerial leaves; *b*, floating leaf blades; *c*, submerged leaves. (After Belzung.)

0°C. In many places the water melts during the day and freezes again at night. The plants pass their existence in ice and icy water.

Marsh Plants, Helophytes.—Marsh plants are those which normally have their roots under water or in water soaked soil, but, like land plants, raise their leaf blades above the surface of the water (Figs. 522, 523, 524). There is no sharp limit between marsh plants and land plants nor between marsh and aquatic plants. Marsh plants and bog plants are confined to shallow, still, or gently flowing water, or to a soil which contains a large amount of water during the greater part of the year. The soil is loose and soft, also usually rich in humus in the form of decayed peat or mud. Many marsh-plants are "amphibious," and susceptible to modification, so that

they can change their structure according as they are submerged or not. The range in leaf modification may be very marked as in certain species of arrow leaf (*Sagittaria sagittifolia*) (Fig. 522). In this species the three forms of leaves easily suggest three different species of plants.

Like aquatic plants, marsh-plants are perennials. Annuals occur only in marshes that are completely dried up during the dry season. They readily develop adventitious roots, and, in many, the stems are

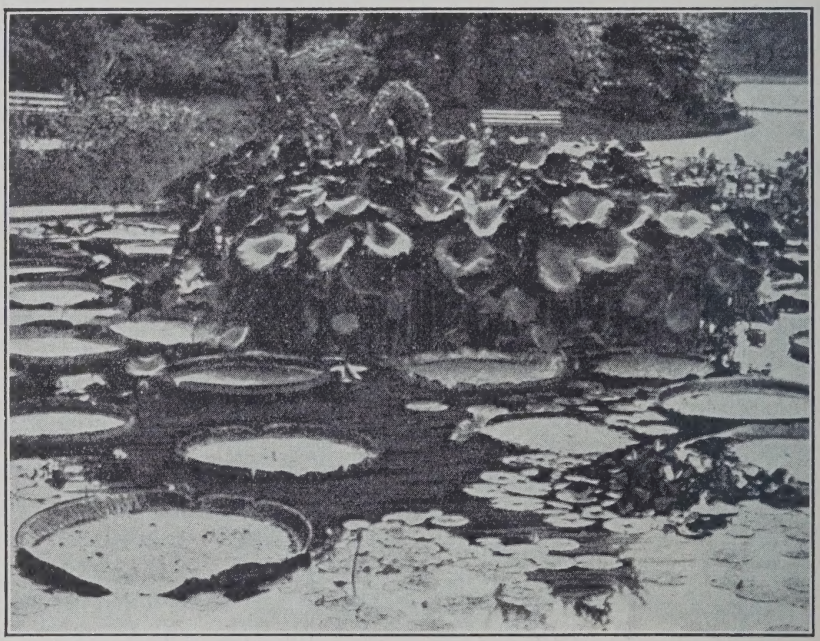


FIG. 523.—An artificial "lily" pond, showing aquatic and marsh types of hydrophytes. Of the floating leaves, the largest with upturned edges are those of the great Amazon water lily (Castalia). The group of plants in the center with the cupped leaf blades raised high above the water on long leaf stalks is the lotus (Nelumbium). (From Coulter's "Plant Relations," Courtesy of D. Appleton & Co.)

thick, fleshy rhizomes. Stems, leaves, and roots are very porous in structure, developing many large internal air spaces by means of which the plants are adapted to meet the scarcity of air in the wet soil. In herbaceous species the vascular tissue is poorly developed inasmuch as the problem of water transport from roots to leaves is very simple even in those cases in which conduction of water is necessary.

Swamp Associations.—In general, marsh plants may be grouped under the following associations: Reed Swamps, Oxalophytes, Swamp Moors, Sphagnum Moors, Heath Moors, Swamp Thickets, and Swamp Forests.

Reed Swamps.—In reed swamps, are found the tall wand-like forms of which the dominant types are cat-tail flags, reed grasses, bulrushes and some other sedges. These grow in rather deep, still water and often characterize the shallow margins of small lakes, ponds, and sluggish streams. In such bodies of water the different plants are likely to be arranged according to depth, the bulrushes standing in the deepest water, and behind them, in order, the reed grasses and then the cat-tails. Intermingled with these may be submerged algae (Chara) and at the proper

FIG. 524.—A reed swamp along the shore of a lake. The three types of the prominent plants are the reed grasses (the tallest), the cat-tails at the right, and the bulrushes, a group standing in deeper water near the middle of the picture. The plant in the foreground at the right is the arrow-leaf (Sagittaria). (From Kerner's "Natural History Plants," A. Blackie & Son Ltd.)

depth, such marsh plants as Pontederia, Sagittaria and water plantains (Alisma) (Fig. 524).

Associations of reed swamp plants are humus soil builders. Each year their dead stems and leaves which grow up from the perennial parts in the mud, and the detritus which collects about them, settle to the bottom and decay, thus forming a layer of humus soil. In this manner the plants tend to build up soil so that in time small lakes and ponds are changed to ordinary swamps and finally into wet meadows (Fig. 525). Instances of such reclamation are seen where bulrushes and cat-tails are

found occupying the wet spots but are shut off from further migration. Some of the great marshes in Indiana and Illinois and elsewhere were formed in such manner.

Oxalophytes, Acid Soil Plants.—Acid soil is usually wet, cold, and, therefore, physiologically dry. It is generally rich in humic acid, or acids found in humus, and becomes moor-like owing to the accumulation of vegetable matter and the formation of peat. The chief cause of the

FIG. 525.—A series of plant communities showing a transition from hydrophyte to mesophytic associations; lily pond, sedges at margin of water, grading into swamp grasses farther back, then shrubs, and finally trees (mesophytes) in the background. (From Coulter's "Plant Relations," Courtesy of D. Appleton & Co.)

physiological dryness lies in the presence of free acids and other dissolved substances which chemically affect the roots or other absorbing organs. Because of this fact some of the plants assume the aspect and structure of xerophytes.

In general the vegetation is abundant, including a wide range of plant families which may be of a rather remote relationship. The plants are not infrequently covered, especially on the under surface of the leaves, with a coating of hairs. Papillae project over the stomata in various grasses, sedges and species of Lysimachia and Polygonum. Coat-

ings of wax, a thick cuticle, mucilage, and other xerophytic characteristics are noticeable features. Moreover the leaves may be round, or flat and erect like those of the Iris and Acorus, or the stems may be leafless and rush-like as in species of Equisetum and the rushes (Juncus, Scirpus).

The plant formations growing on acid soil are treated under such heads as swamp or low moors, grass-heath, high moors, moss and Lichen tundras, dwarf-shrub heath, and high bushland.

Swamp Moors.—The term moor usually refers to a meadow-like expanse of swampy ground. Swamp moors include ordinary swamps, bogs, and marshes. There is, as a rule, little standing water. The water is usually rich in nitrates which are used by the plants in making proteins. Consequently the vegetation is dense and the made soil is black and rich in humus. Dominant plants are grasses and sedges which give a meadow-like appearance to the area. It should be remembered that many other species of plants adapted to such places, (buttercups, mosses) grow among the sedges and grasses. In the north, where temperature conditions are unfavorable to sedges and grasses, the moor may become a bed of moss which contributes so largely to the formation of *peat*, a forerunner of coal. Peat consists of partly decayed Sphagnum moss and the dead parts of other plants which are kept from complete decay by being submerged in the water. Under such conditions, fungi and bacteria which bring about decay do not thrive. The soil becomes acid and peat may be formed instead of humus.

Sphagnum Moors, Bogs.—In this association the dominant plant is Sphagnum, or peat moss. The grasses and sedges of swamp moors being absent, the sphagnum forms a dense turf over the deep, black, soft water-soaked mud, which becomes springy when one walks over it. Because of the springy, trembling character the name, "quaking bog" is applied to such areas. It is in the peat bogs that many very interesting insectivorous plants (Drosera, Dionaea, Sarracenia, etc.) and orchids may be found. The water in a Sphagnum bog is poorer in materials from which plants manufacture protein than the water in a swamp moor.

Heath Moors.—Heath moor and mountain moor are terms used in a descriptive rather than in a scientific sense. The peaty soil supports a dense growth of heaths (Ericaceae) and the bracken fern. In the uplands (England, Scotland) where the peat is deep and acid, the dominant ground cover is the common heather (*Calluna vulgaris*) which, when in bloom, suggests a great expanse of common red clover in bloom, especially if the clover be viewed at a distance. The seed of the heather affords food for grouse and other birds.

Swamp Thickets.—These associations are similar to swamp moors. However, the conditions are more favorable for the growth of certain

shrubs and trees than in the swamp moor. The trees are uniform in type consisting mainly of willows, birches and alders. Swamp thickets were probably derived from swamp moors.

Swamp Forest, Tamarack Swamp, Cypress Swamp.—In a sense a swamp forest may be a kind of swamp moor in which is present certain types of trees. Here we find larches or tamaracks (Larix), hemlocks, pines, and junipers. Tamarack swamps are usually more limited in extent than those of the hemlock, pine, etc.

Cypress swamps are confined chiefly to the south, and the dominant tree is the bald cypress, Taxodium (Fig. 95). Cypress swamps extend northward in the Mississippi valley to the south western corner of Indiana.

Xerophytes.—While hydrophytes include those types of vegetation which live in relation to the *maximum* water supply, xerophytes are those plants which live in relation to the *minimum* water supply. They are the dry land or desert plants, such as have been commented upon in the paragraphs treating of deserts and steppes. No sharp line can be drawn between these two groups of habitats, for they often merge into each other. In a xerophytic formation there may be localities which are purely hydrophytic, and xerophytic habitats limited in extent are to be found in the region of hydrophytic formations.

Bare Rock Associations, Lithophytes.—Lithophytes are those plants which are able to colonize steeply inclined or perpendicular, bare rock. They belong exclusively to the Thallophyta. Algae and Lichens are undoubtedly the first colonists. Among the hardiest of all plants they easily rank first. Bare rock communities vary immensely, owing to differences in the climate and in the character of the rocks. All are, in a measure, rock disintegraters and soil makers. They prepare a more favorable substratum for larger forms including small flowering plants.

Crevice Plants, Chasmophytes.—Only lithophytes grow on rocks that are without cracks or crevices. Chasmophytes are those rooted in cracks and crevices of rocks that are filled with detritus. Into the crevices, particles of earth are blown by the wind, and soil is washed into the cracks by water. In the soil thus accumulated, plants become established and their dead fragments add to the soil supply. Soon earth worms and other small animals burrow in the humus and improve it. The richest crevice flora is found upon rocks which retain water, such as lime stone. The plants range all the way from mosses and liverworts to the spermatophytes. Of the ferns, the cliff brakes (*Pellaea atropurpurea* and *P. blanda*) are the most prominent especially upon limestone ledges and cliffs. In fact they are regarded as sure indicators of the presence of limestone. However, they may grow upon sandstone. Succulent and rosette plants (Sedum and Saxifraga) are common, along with the

alum root (Heuchera), bishop's cap (Mitella), columbine, wind flowers, wild gooseberry, Hydrangea, and a profusion of others. In fact, the face of certain limestone cliffs in the Central States suggest a small botanic garden hung upon a wall.

FIG. 526.—A view of an active dune from the windward side. (Courtesy of Mr. Orpheus Moyer Schantz in the National Geographic Magazine.)

Crevice plants range all the way from xerophyte to mesophyte.

Sand Plants, Psammophytes.—Vegetation on sand varies greatly, depending upon atmospheric conditions and the nature of the soil, especially its humidity. Plant life on sandy beaches near the shore of lakes and the seacoast where the moisture reaches the surface is very different from that in localities where there is a considerable depth of dry sand above the water-table, or saturated moisture line. Passing from the water's edge toward higher levels, we have (1) the strand vegetation along the shore; this may be followed (2) by wind blown elevations of sand or dunes, and beyond the dunes (3) sandy fields. When these three asso-

ciations occur in the same locality the plants of the different areas merge into one another. When dunes are absent, then beaches pass gradually into sandy fields.

Strand Flora.—Beach or strand floras are distinctively characteristic and generally poor. The plants may occur in tufts or they may consist chiefly of creeping or trailing species. Although water is abundant, it disappears quickly, and the soil is poor. The light is intense and on the whole the conditions for plant growth are unfavorable.

Dunes.—Dunes are elevations of sand blown up by the wind from the shores of lakes or of the sea or in fact in any sandy, wind-swept area. They occur in all parts of the world. In the United States dunes are common along the Atlantic coast in Massachusetts, New Jersey, Virginia, North Carolina and Florida. They are present also along the Pacific coast, in Nebraska, Colorado (San Luis Valley) and along the eastern shores of the Lake of the Woods and of Lake Michigan.

Fine sand blown by the wind from the shore will form piles or drifts upon encountering obstructions just as wind driven snow will form snow drifts under similar conditions. Here we are concerned with dunes in which plant life plays an important role, and the comments which follow pertain chiefly to the plant life of the great sand dune region extending along the southern and eastern shores of Lake Michigan from Dune Park, Indiana, to the northern end of the lake.

Here the dunes are billowy elevations, or hills of sand heaped up by the prevailing winds blowing from the lake shore landwards.

In certain localities the dunes have attained an elevation of 400 feet or more, and a width of three fourths of a mile landward from the shore. Established or stationary dunes are covered by forest vegetation. On the windward slopes evergreens dominate, while on the leeward side deciduous trees and shrubs prevail.

Active Dunes.—Active dunes are those which are in process of formation, and which are constantly shifting. A bunch of perennial grass, or a bush growing upon the sand-swept beach above the highest wave line will collect and retain a small pile of sand which slopes off on the leeward side. With the upward growth of the plant, this young dune will become larger and higher. Many such small dunes forming near each other will eventually result in a large dune or a dune complex, which moves slowly but continually in a leeward direction.

In the formation of a dune a peculiar type of vegetation is necessary. The most effective plants are those known as "sand-binders." Their underground parts, rhizomes and roots, are well developed, extending long distances horizontally and penetrating deeply in search of water. Chief among the dune builders are the grasses, *Ammophila arenaria* or

beach grass, *Calamovilfa longifolia*, *Agropyron dasystachyum* or reed-grasses, *Elymus canadensis* or wild rye, the willows, (*Salix syrticola* and *Salix glaucophylla*), the willow poplars or cotton woods (*Populus deltoides* and *Populus balsamifera*), the red-osier dogwood (*Cornus stolonifera*) and the sand cherry, (*Prunus pumila*). About the only plant which is said to flourish everywhere on the dune is the succulent annual, *Corispermum hyssopifolium*.

Another characteristic of dune producers is their ability to grow up through the sand as they become engulfed. From the buried branches

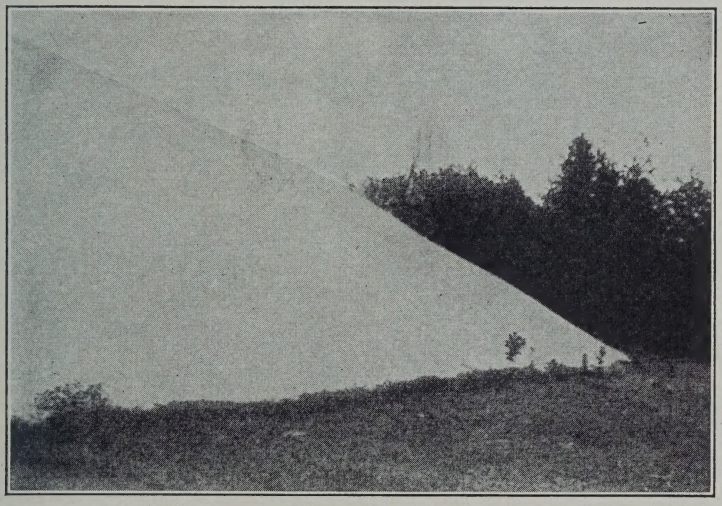


FIG. 527.—The leeward slope of a moving sand dune. (Photograph by A. B. Klugh in Clute's "Agronomy," Ginn & Co.)

of the cotton wood and other trees roots will develop which enable the trees to secure moisture from the sand at higher levels.

Active dunes are found in Dune Park, near Michigan City, Indiana and at other points farther north, especially near the mouths of rivers (Figs. 526, 527).

As the winds sweep up the windward slope of the dune their velocity and carrying power are diminished. The fine sand falls at the top of the dune and rolls down the lee side under the force of gravity alone. The result is a steep leeward slope, the gradient being about 30° (Fig. 527). The windward slope has a more variable gradient (Figs. 526, 528).

As the dune becomes higher and drier, and as the life of the plants is indefinite, the plants die and the sand is blown away. The dune or dune complex moves slowly but continually in the direction of the prevailing

wind, destroying all antecedent vegetation standing in its path (Fig. 528, 529). The influence of the encroaching dune varies with the rate of movement, the height above the country invaded, and the nature of the vegetation. The burial of forest trees is a common phenomenon (Fig. 529). The dominant trees in the path of the advancing dunes are the scrub pine (*Pinus banksiana*), the hemlock (*Tsuga canadensis*), the black oak (*Quercus velutina*), and the maple (*Acer saccharinum*). These trees perish long before they are completely buried. As the dune passes on, the dead

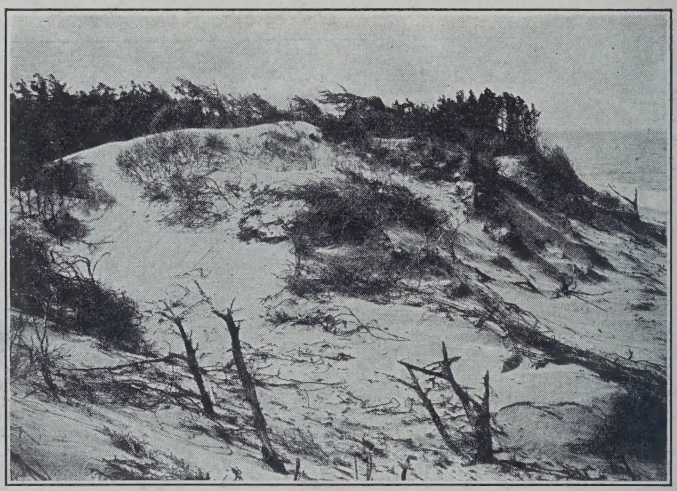


FIG. 528.—Moving sand dunes from the windward side near Cape May, N. J. where once the whaling town of Portsmouth stood. In the foreground, red cedars buried and partly uncovered by the wind. (From Bull. 24, Bureau of Forestry, U. S. Department of Agr.)

trees may be uncovered, when their ghastly trunks, rising above the waste, appear as mute reminders of the destructive action of the traveling sand (Fig. 530).

In the Dune Park region, swampy ground often lies in the path of the advancing dune. Although most of the vegetation is destroyed at once, *Salix glaucophylla*, *S. adenophylla*, and the red-osier dogwood (*Cornus stolonifera*) may adapt themselves to the new conditions by elongating their stems and sending out roots from the buried portions. In the dune complex, reverse winds may uncover the partly buried trees or uproot them almost completely (Fig. 528, 530).

The Established Dune.—Not until the distance from the shore becomes greater, and the wind weaker, and protection is provided by other dunes in the complex, does vegetation begin to capture and clothe the dune

(Fig. 531). Among the first plants to appear upon the lee side of the slowly moving dune are the grasses, the common milkweed and the tall Equisetum. Plants tend to creep up the slopes by vegetative propagation. Antecedent vegetation and new arrivals work together. In a few

FIG. 529.—The leeward side of a travelling sand dune encroaching upon antecedent vegetation. Large forest trees are being engulfed. (Courtesy of Mr. Orpheus Moyer Schantz in the National Geographic Magazine.)

years the lee side becomes overgrown by such trees and shrubs as the linden, frost grape, choke cherry, red-osier dogwood, blue berries, etc. Shrubs suppress herbs. Eventually linden trees, oak, ash, walnut, and sassafrass together with the climbing plants, lianas, such as the frost grape, poison ivy, Virginia creeper and wild smilax, produce a forest (Fig. 531).

On the established windward slopes, the development is different from that just described. The soil is about the same but the air is drier. Annual and biennial herbs are the first to grow, the bug seed (*Corispermum hyssopifolium*) leading. In time, small shrubs including the bearberry

(Arctostaphylos), *Juniperus communis*, and *J. sabina procumbens*, constitute the beginning of the evergreen flora. In turn the low shrubs give way to such coniferous trees as *Pinus strobus*, *P. banksiana*, *P. resinosa*, *Thuja occidentalis*, *Abies balsamea* and *Juniperus virginiana*. Beneath the trees, grow the dune shrubs just mentioned. Along the shore of the lake,

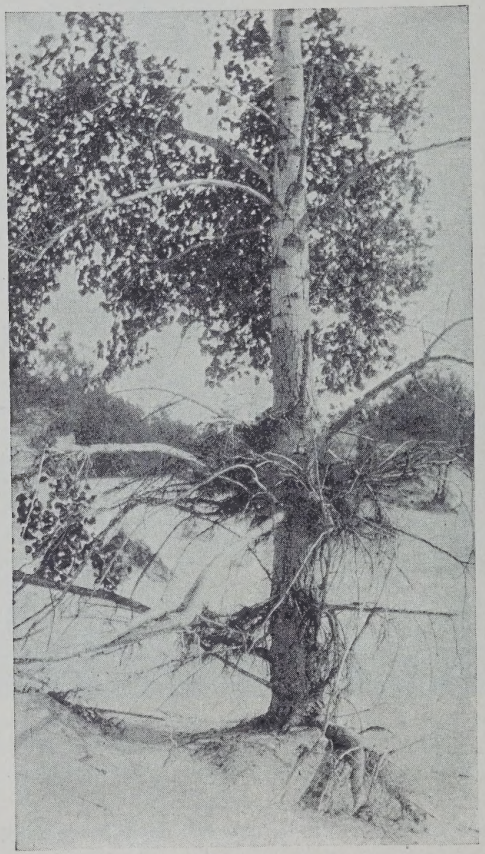


FIG. 530.—A cottonwood tree which was buried in the sand to the top of the dark line and uncovered later. Roots had developed from the buried branches which are again producing leaves. (Courtesy of Mr. Orpheus Moyer Schantz in the National Geographic Magazine.)

bush land composed of black oak (*Quercus velutina*) replace the coniferous forest in certain localities.

The stationary dunes along the eastern shore of Lake Michigan are dune forests. The eastern reaches of this vast range of sand hills present varied and interesting habitats, each with its rich and peculiar flora.

The numerous ponds, swamps, bogs and shrub habitats are rich in the vegetation characteristic of such localities. Dry hilltops with their ground cover of bearberry and other xerophytic shrubs are often but a few minutes walk from the low grounds with their tussocks of Osmunda, and the Sphagnum bog with its interesting sundew and pitcher plants.

Evergreen Coniferous Forests.—The scale-like leaves of the true cedars (Cupresseae) and the needles of the pines and pine-like conifers (Abieteae) are representative of coniferous foliage, which afford a relatively small surface for the evaporation of moisture. As a further check on transpiration the epidermis is strongly cuticularized and the stomata

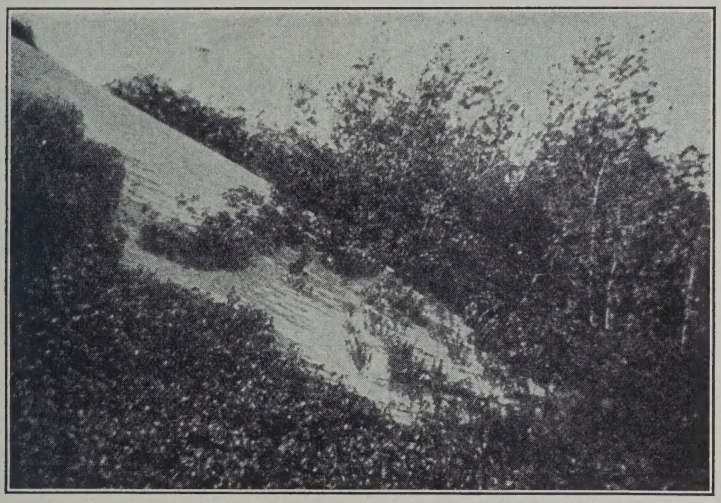


FIG. 531.—A dune being captured by vegetation. (From Clute's "Agronomy," Ginn & Co.)

sunken. In further keeping with their xerophytic nature the conifers have few or insignificant root hairs.

Coniferous forests occur under diverse climatic conditions, with the exception of a torrid dry climate. They are most extensively distributed over the northern hemisphere, becoming much less prominent in warmer climates. While the soil upon which conifers grow varies greatly, it is, as a rule, physically and physiologically dry. In warmer regions conifers prefer a porous, warm, sandy soil; in colder regions they grow upon nearly all kinds, varying from dry rocks and sand fields to wet marshy ground. Another feature correlated with a xerophytic character in gymnosperms is the structure of the wood. Here the wood is composed of narrow tracheids only, and it is much less capable of transporting rapidly large quantities of water than the wood of broad-leaved dicotylous

angiosperms whose wood contains large vessels. It is not improbable that the xerophytic character of gymnosperms is more the result of racial development than an ecological adaptation.

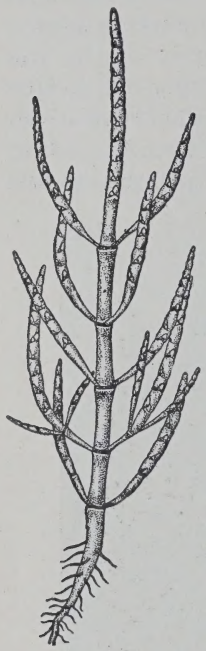


FIG. 532.—The Samphire (*Salicornia herbacea*) of our seacoast. (From Schimper's, Plant Geography," Clarendon Press.)

The undergrowth which clothes the ground in coniferous forests consists of perennials. Among the dwarf shrubs are Vaccinium, Juniperus, Arctostaphylos, etc. A number of genera possess creeping rhizomes, such as Monotropa, *Goodyera repens*, and other angiosperms, together with the bracken fern (*Pteris aquilina*), species of Dryopteris and others. The northern coniferous forest contrasts also noticeably with a dictoylous forest in the abundance of shrubs which have fleshy fruits.

Various kinds of coniferous forests are recognized on the basis of the dominant kind of trees, as pine-forest, mixed coniferous forests, etc. Each of these possesses a certain characteristic under growth and other features too numerous to mention here.

Larch forests are the *deciduous* coniferous forests of northern regions. Because of this fact they are the most hardy. Larch trees give rise to forests in the polar region of Siberia, being adapted to the short growing season, and less dependent upon the cold of winter than upon the heat of summer. Like the pines they are *light-demanding*.

Halophytes.—The word means "salt plants." Halophytes are those plants which are able to grow in water or upon soil containing certain salts which make it impossible for most plants to live. They occur near the sea shore, around salt springs, on alkaline flats or wherever the soil is saline. The garden Asparagus is in a measure a halophyte, as it thrives well when the soil contains sufficient salt to be detrimental to other garden plants in general.

Some halophytes resemble succulent desert plants in the absence of leaves and in the development of succulent stems (Fig. 532). Succulent stems conserve moisture and the absence of leaves reduces the evaporating surfaces. Plants absorb much less water from soil and from pond water containing certain salts and acids than they do under ordinary conditions.

Mangrove swamps, beach marshes and meadows, salt steppes, salt and alkaline deserts are all associations of halophytes.

Mesophytes.—These are the plants found where optimum conditions of soil and air make possible the highest type and most luxuriant growth

of plant life. The soil is well drained and well aerated. Mineral salts are present in moderate quantities and the air is moderately humid. The rainfall is more evenly distributed over the different seasons.

FIG. 533.—Alpine vegetation. Note the low dense growth and conspicuous flowers. (From Kerner's "Natural History of Plants," A. Blackie & Son Ltd.)

Two types of mesophytic associations may be recognized, although they may probably be as distinct from each other as mesophytic and xerophytic communities. One type is composed of low vegetation,

FIG. 534.—Plants of the rock-rose (*Helianthemum*) illustrating the effect of low ground and alpine conditions. A, a plant grown upon low ground, showing the open habit, elongated branches and comparatively large and well-separated leaves. B, the same plant in alpine condition drawn to the same scale as A. C, the same plant as B, magnified. The short and compact habit appears in striking contrast with that of the low-land form. (From Coulter's "Plant Relations," Courtesy of D. Appleton & Co.).

chiefly grasses and herbs; the other is composed of trees and other woody vegetation.

Arctic and Alpine Mat-Grassland and Mat-Herbage.—In polar regions and above the tree limit in high mountains, the vegetation covers the ground in dense carpet-like mats which consist chiefly of grasses and grass-like monocotylous plants in moist localities and of herbaceous dicotyls in drier places.

FIG. 535.—A small natural meadow surrounded by trees and shrubs. (From Schimper's "Plant Geography," The Clarendon Press.)

The soil is usually rich in humus and well-watered from the melting snow. The growing season is short. The temperature is low at times, especially during the night, and the illumination is intense. In fact the conditions do not permit the development of trees and shrubs or even tall herbs, but they favor a rapid growth in the plants adapted to such surroundings. As a result, the vegetation presents a fresh-green, dense covering which, if typical, is low and soft. Because of this fact the term *mat-vegetation* is applied.

The majority of the species are perennials. Many possess rhizomes which grow beneath the surface of the soil. The broad-leaved rosette habit is common among the dicotylous species. This is presumably the

result of the low stature and intense light. The color of the flowers is intense and brilliant. One is impressed with what seems to be the large size of the flowers as compared with the size of the plant (Fig. 533). The large size is more apparent than real, for a flower on a plant of small stature will appear larger than one of the same size borne by a larger plant.

Mat-vegetation in which the grasses are predominant afford excellent pasture land. If the grass be tall enough to cut, the region is referred to as a mountain or alpine meadow.

The effect of the alpine conditions upon the habit of the plant is seen when one compares an individual of the same species grown on low ground. In Fig. 534, A, is shown a portion of the rock-rose (Helianthemum), grown at a low altitude, with elongated stems, open habit, and comparatively large and well separated leaves. The same plant in alpine conditions is shown at B, drawn to the same scale, and enlarged at C. The short and compact habit appears in striking contrast with that of the low-ground form.

In arctic mat-grassland there is generally an intermingling of monocotylous and dicotylous perennial herbs. When the dicotylous species dominate over the grasses, there arises a different type of flora which is designated as mat-herbage or mat-field. It is said to be more widely distributed than grassland in polar regions and on high mountains.

Meadows.—This term does not refer to fields of grass or artificial grasslands under control of man commonly called meadows. Meadows are native, fertile areas containing a mixture of grasses and flowering herbs, the former being the predominant type. Such areas are often developed in connection with forests and they may occur side by side (Fig. 535). To ascertain the definite conditions which determine the one or the other is an interesting problem.

The greatest meadows of the United States are the rich prairies which extend from the Mississippi eastward to the forest regions of Illinois and Indiana. Prairie vegetation consists chiefly of grasses, which often form a very dense turf, and perennial flowering dicotylous herbs. The flowering herbs are generally tall with brilliant and showy flowers (Fig. 536). The more numerous among them are species of wild sunflower, rosinweed, aster, golden rod, indigo plant, lupine, bush clover, Amorpha and very many others. In mid-summer a prairie presents a different picture from that of a monotonous expanse of mixed grasses.

The absence of trees in a soil suitable for their development presents a difficult problem. A common explanation is that prairie fires which occurred from time to time destroyed the trees which may have gained a foothold. It is more probable that the causes were natural rather than artificial. The dry prevailing winds from the west which sweep over

these prairies bring about extremes of heat and drought in summer in spite of the character of the soil. Under such conditions, seedlings of forest trees could not establish themselves. Isolated groves or wooded tracts in the midst of a stretch of prairie offer the best evidence looking toward a solution of the problem. These wooded areas occurred where there were springs or where the soil did not dry out so completely, as may be seen at present wherever such groves still exist.

FIG. 536.—Fertile prairie east of the Mississippi River. Note the dense cover of grass interspersed with clumps of herbaceous perennials (showing dark in the picture). These lands are rapidly passing under cultivation. (From Coulter's "Plant Relations," Courtesy of D. Appleton & Co.)

Mesophytic Forests.—The highest expression of a mesophytic flora is found in the dicotylous forests developed under the most favorable conditions. Of these there are two types, the *evergreen dicotylous forests including the tropical rain-forests*, and the *deciduous dicotylous forests.*

Evergreen Dictoylous Forests.—As the name implies any crop of leaves of an evergreen remains on the tree longer than a year or until the next crop following appears, although in many of these forests species occur which are leafless for a longer or shorter period. Evergreen dicotyl-

ous forests occur not only in tropical and subtropical regions, but also in the cold temperate zone of the Southern Hemisphere.

The Tropical Rain-Forest.—A tropical rain-forest represents the grand "climax in the development of vegetation in the whole world." The moist, porous soil very rich in humus and the continual warmth and humidity of the air, constitute an environment which tends to force plant growth to the utmost degree. The number of species is very large,

FIG. 537.—Epiphytes upon a branch of a tree in a tropical rain-forest. Note the various kinds of plants with their dangling aerial roots. (From Schimper's "Plant Geography," The Clarendon Press.)

and the individual plants are so numerous that space is lacking for all to be connected with the soil. As stated by Humboldt, "forest is piled upon forest." The tallest trees are unbranched up to a height of 40 or 50 meters. Growing among these are trees of smaller stature, and beneath these are slender, thin-stemed, low palms, tree ferns, other shrubby plants, and huge herbs which may attain a height of 4 or 5 meters. If there still remain space and the light reaches the ground, smaller ferns, Selaginellae, mosses, etc., may be present. In certain places the light is too feeble and the ground is consequently bare, or occupied by bizarre saprophytes

or root parasites. In addition to those mentioned, gigantic lianas climb upon the trees, lashing themselves to the trunks by cord-like, clasping roots. In addition to all these which are rooted in the soil, hordes of epiphytes attach themselves to trunks, branches, and leaves (Fig. 537).

The buds do not possess dry bud scales as do those of our forests. The peculiarities of roots, trunks, bark, and leaves are so numerous and varied that space prohibits even their enumeration. The leaves assume an extraordinary number of shapes. It seems that where rain falls daily or almost daily, the ability to dry readily would be an advantage if not a necessity. This is accomplished by the presence of a smooth cuticle, which cannot become wet. Many leaves which are capable of being rendered wet, end in long, tapering points, known as *drip tips*, as in the fig, *Ficus religiosus* (Fig. 538). The leaves are directed downwardly, and the long slender tips enable the water to flow away rapidly. Frequently channelled veins occur which serve to convey water to the pointed tip.

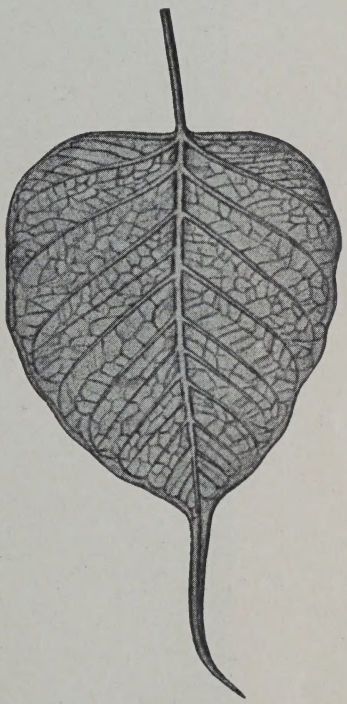


FIG. 538.—A leaf of *Ficus religiosa* ending in a "drip tip." (After Stahl.)

Deciduous Dicotylous Forests.—This type of forest is one in which the trees are leafless for a longer or shorter season of each year, and are in foliage during the remaining seasons, totalling five to eight months. These two conditions are correlated with the climate, the leafless period coinciding with the winter season in temperate and cold regions, but with the dry season in the tropics. There is consequently a season of foliation and one of defoliation. The growing ends of the shoots terminate in resting buds covered with corky or cuticularized scales. These winter buds often contain a large part of the following season's growth. The twigs and branches are protected by layers of cork. The waterproof bud scales and the corky layer of the bark reduce transpiration to the minimum. The bud scales afford efficient protection against the desiccating action of freezing and thawing.

During the entire winter season, or during the period of defoliation, the plants are in a xerophytic state.

The beginning of the seasons of foliation and defoliation are each accompanied by a notable feature. The period of growth in the spring is ushered in by a flash of pale yellowish-green foliage when the naked

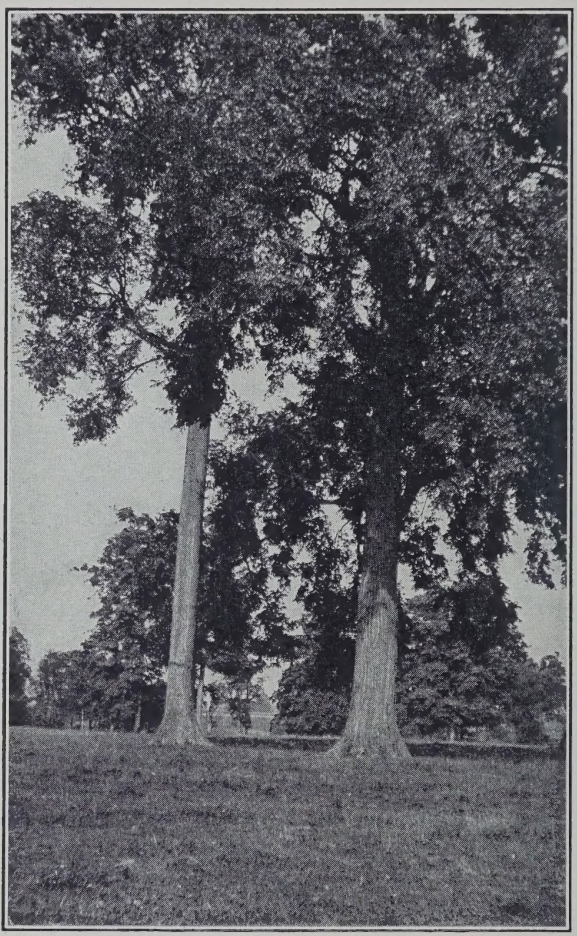


FIG. 539.—Two matchless white elms. (Photograph by Glenn W. Blaydes.)

twigs become clothed with verdure. The complete change is frequently made in a few hours or in a few days.

The close of the season of foliation and the beginning of the leafless and xerophytic state are marked by a riot of leaf colors which appear as suddenly as did the verdure of spring. The gaily colored leaves in such trees as the hard maples, dogwood, sumac, sourgum, etc., remain upon the

branches for a few days only, when all fall, leaving branch and twig completely defoliated.

In the spring, or at the beginning of the growing season, the dormant buds unfold, revealing the young leaves or leaves and flowers, borne upon

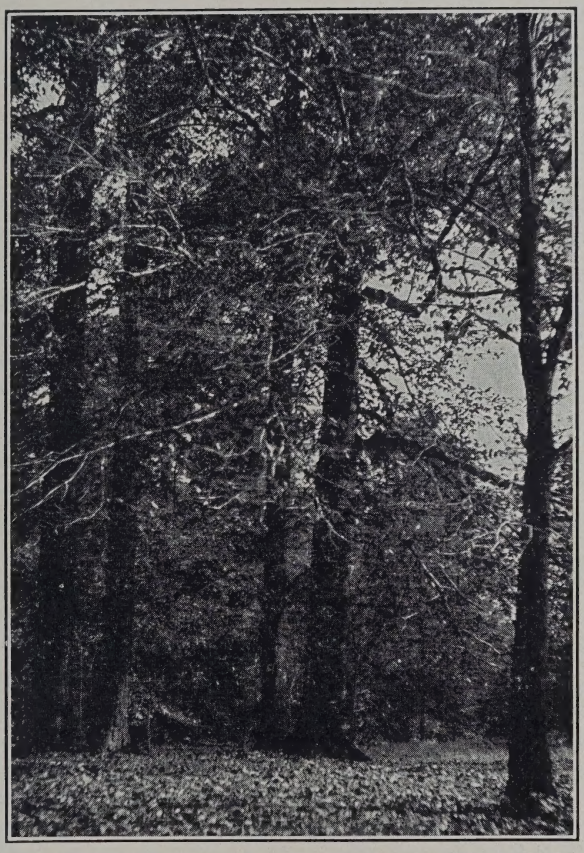


FIG. 540.—A peep into a beech-maple primeval forest. (Photograph by Glenn W. Blaydes.)

tender green shoots. During the period of foliation one sees at all times tender yellowish-green leaves and stems. As the leaves mature they assume the shade of deeper green characteristic of the plant. With the advance of the season the twigs develop their protective layer of cork, and take on the dull colors of mature and permanent parts. At the same time winter buds are gradually developing within, those structures which will appear the following spring.

Deciduous forests have a special interest for us inasmuch as they represent the climax of plant life developed under primeval conditions in the eastern part of the United States. Here were vast areas of the magnificent hardwoods constituting a natural resource of inestimable value. Only comparatively small areas remain. Among the dominant trees are the beech, maples, oaks, hickories, ashes, the black walnut, tulip tree, elm, (Fig. 539) linden, wild black cherry, hackberry, chestnut, black locust, honey locust, and others ocurring chiefly upon well drained soil (Fig. 540). Along the rivers and creeks and upon the alluvial flood plains adjacent thereto were gigantic sycamores, willows, cotton-woods (Populus) and others.

In ours and in other countries certain of the trees mentioned occurred in pure stands upon areas of a size sufficient to merit such names as beech forest, beech-maple forest, oak forest, birch forest, ash forest, etc.

Among the great trees, grew those of smaller proportions, together with numerous shrubs, and herbs. Of these, the flowering dogwood (Cornus), iron wood (Ostrya), water beech (Carpinus), Kentucky coffee tree (Gymnocladus), papaw (Asimina), service berry (Amelanchier), and Sassafras were common.

The herbaceous flora of a deciduous dicotylous forest differs strikingly from that in a tropical rain forest. The rich vernal herbaceous flora of our woodlands is unsurpassed in beauty and variety. In the vast majority of the perennials the bulk of the plant grows in the ground in the form of rhizomes, bulbs, corms or tuberous roots. They are styled geophilous plants. Each spring the underground parts send up leafy vegetative shoots which bear flowers and fruit, and then disappear. Their season of vegetative activity above the soil is very short in comparison with the period of the dormant or xerophytic state. Appearing early, they receive the benefits of full illumination, and become thereby removed from competition with overshadowing trees and shrubs.

Of the early "spring flowers" so conspicuous in the beech-maple woodlands are species of Trillium, the lamb's tongue or dog's tooth violet (*Erythronium*), the bloodroot (*Sanguinaria canadensis*), Dutchman's breeches (*Dicentra*), Hepatica, the spring beauty (*Claytonia*), Indian turnip (*Arisaema*), crow's foot (*Dentaria*), celandine poppy (*Stylphorum*), May Apple (*Podophyllum*), fire pink (*Silene virginica*), and others too numerous to mention.

A few lianas are present, the larger being the wild grape vine, the Virginia creeper, the bitter sweet (Celastrus), and the poison ivy (*Rhus toxicodendron*).

The herbaceous ground cover in all tree associations varies with the habitat of the forest area.

From the dawn of life upon the surface of the Earth to the present, the development of plant life has continued steadily through eon after eon. Mighty floras have come and gone. Climax after climax has appeared and disappeared, until, at the present time, we find in our remaining bits of primeval forest (that undisturbed by man) the last and latest forest climax with its majestic tulip trees, its graceful elms, its mighty oaks, sturdy beeches, and beautiful maples. Beneath all these, there spring up each and every year the rich vernal flora, lending its charm and beauty in marked contrast to the brown landscape of the passing season.

TOPICS FOR REVIEW AND DISCUSSION

What two climatic factors determine in a large measure the distribution of large areas of plant life? Which of these factors is more influential?

Locate the forest regions of the earth; of North America.

How do mountain forests differ from those of low lands?

Where are the endemic Sequoia forest areas located at present? Did trees of the genus Sequoia occupy a larger area of the land surface of the globe? In what geological epoch?

Giant Sequoias and the cedar of Lebanon will not thrive in the Ohio Valley but they grow well in England and Scotland. Why?

Why are few or no trees found in the great prairies, steppes, and pampas?

How do you account for the prairies (meadows) of Indiana and Illinois?

Locate the desert regions of the earth.

Where in the Western Hemisphere does rain rarely fall?

Give the important characteristics of desert vegetation.

What is chapparal?

Why is the term "sage brush" applied to a number of plants which differ in relationship?

What are savannahs or semi-deserts? Where do they occur chiefly? How do they differ from typical deserts?

What are tundras? Locate the great tundra regions of the globe.

Are tundra plants sometimes found outside of tundra regions?

To what depth does the ground thaw in summer in the arctic regions?

What is Iceland moss? Is it of any economic importance?

What constitutes reindeer pasturage?

What animal industry has recently sprung up in Alaska?

Are there beautiful showy flowers such as orchids, etc., in Alaska?

What is plant ecology? Animal ecology?

Name the ecological communities as determined by the maximum water supply.

What are mesophytes?

Distinguish between a pure aquatic and a marsh plant.

Characterize the vascular system of aquatic and marsh plants.

How does the ground tissue of large marsh plants differ from that of the clover or bean plant?

There is little or no air in the mud at the bottom of a pond. How are the tissues of the rhizomes of the white water lilies aerated?

Name some of the smallest floating aquatics which bear seeds. Some of the floating Pteridophyta.

What small floating Pteridophyte bears no roots?

How many different forms of foliage leaves may marsh plants possess? Name some marsh plants possessing such leaves.

Name plants which have floating devices. From what parts of the plant body may floating devices develop?

Do any aquatic and marsh plants capture insects? If so how are the insects caught and held?

What is plankton?

Explain the meaning of the expressions, "red rain," "red snow," "brown snow," "green snow."

Are aquatic and marsh plants chiefly annuals or perennials?

What is meant by the term "amphibious" plant?

Where and in what form do many marsh and aquatic plants spend the winter?

Explain how plants will change a shallow lake into a marsh.

What is a flood plain?

What is the source of alluvial soil.

What kinds of trees characterize flood plains in your locality?

Do you know of any plants which survive being frozen in ice all winter?

What is a reed swamp?

What is a swamp thicket?

What is a bog?

What is a moor? A swamp moor?

What are oxalophytes?

What makes soil acid?

Why are cold acid soils physiologically dry?

Do bogs occur on the slopes of mountains?

What is a heath moor?

Where do extensive heath moors occur?

What is a swamp forest?

What is a cypress swamp? Where do they occur in North America?

What are "cypress knees"?

For what uses is bald cypress lumber valuable?

What is the tamarack tree? A tamarack swamp?

What are xerophytes? Do all xerophytic plants grow in deserts?

What is the xerophytic condition of a plant?

In winter our deciduous trees may be said to be in the xerophytic condition. What is meant?

What are lithophytes? To what groups of plants do they chiefly belong?

In what respect do lithophytes prepare conditions for larger plants?

What are crevice plants?

What is meant by the expression, small botanic garden hung upon a wall?

What are strand plants?

Are strand floras rich or poor in the number of species? Why?

What is a sand dune?

Where do large sand dunes occur in North America?

Do sand dunes occur where there is no vegetation? If so, where?

Compare the formation of a sand dune with the formation of snow drifts.

Referring to plant life, what are sand binders?

What is an active dune?

Do dunes travel in the windward or leeward direction?

What is an established dune?

Name some herbs, bushes, and trees which are found on the dunes east of Lake Michigan.

How do dunes destroy vegetation?

Explain how and under what circumstances vegetation captures and halts the progress of dunes.

Is the bearberry plant used in landscaping?

Are dunes ever covered with forest trees?

What dunes have you seen or visited?

Having formed an idea of a dune from descriptions and pictures in books before you had seen one, what was your mental reaction when brought face to face with a great dune?

Where did the sand come from that forms the dunes along the east shore of Lake Michigan? (The lake was there before dunes were present.)

What is an evergreen forest? An evergreen coniferous forest?

Are pine forests better adapted to dry places than broad-leaved forests?

Will the trunk of a pine tree conduct water as rapidly and in as large quantities as the trunk of an elm tree?

Do you regard coniferous trees as being xerophytic?

Do you think coniferous trees transpire as much water as elm or oak trees?

What conifers are the most resistant to cold?

What conifers demand much sunlight? Name some which will tolerate a considerable shade?

What is meant by the term "salt plants"? What other ecological group of plants do they resemble?

Name a garden plant which is a halophyte.

Where do mangrove trees grow in the United States?

To what ecological group do they belong?

It is said the roots of the mangrove must grow where water is salty. How would you account for mangrove trees growing some distance from the sea in Florida?

What are mesophytes?

Why do mesophytes represent the highest type of vegetation which has been developed upon the earth?

What ecological type of native plants is dominant in your locality?

Distinguish between a natural meadow (not developed by man) and a prairie.

What are mountain meadows?

How will some Alpine plants develop when transplanted to low lands?

How would you explain the origin of the praries which existed in Indiana and Illinois?

Distinguish between a deciduous dicotylous forest and an evergreen dicotylous forest. Where are the latter found?

Are the buds of the trees in the tropical rain-forests quite like those in the deciduous forest?

Do spring flowers, such as Trilliums, bloodroot, Dutchman's breeches, May Apple, celandine, poppy, etc., occur in tropical rain-forests?

What are epihytes? Where do they flourish in greatest profusion?

Who was Humboldt? What did he mean by the expression, "forest is piled upon forest"?

What are lianas? Do any occur in your locality? Where do they grow most luxuriantly?

What are "drip tips" as applied to leaves? Are they of any value to the plant?

What two very noticeable phenomena appear each year in a deciduous forest?

Is there a movement of sap upwards in a deciduous tree during the winter?

What enables the deciduous trees to come so suddenly into foliage in the spring?

Name four or five native trees in your state which you think yield the finest hard wood lumber?

What is the finest soft wood conifer in North America? What parasitic fungus threatens its existence?

In what state in the Union were there valuable chestnut forests? What has happened to those forests?

What three native deciduous trees in the Ohio Valley supply the finest wood (especially veneering) for cabinet work?

From the viewpoint of the forester, what are "weed trees"? Name several.

Why were fine hard wood trees such as oak, walnut, and tulip poplar (yellow poplar) rolled into heaps and burned in Indiana, Ohio, and Kentucky one hundred years ago when there was a good market for such lumber in Europe?

In your state what would you recommend be done with the poor, worn out, and eroded land upon which tillage is a very difficult or unwise undertaking?

What sort of trees may be grown for paper pulp in your locality upon swampy, untillable land?

Do you think that the giant Sequoias left standing in California are of greater commercial value alive than converted into lumber at any market price?

What is the value of forest reservations in any state or country?

What political divisions of the northern hemisphere have made the greatest strides in scientific forestry?

What is an ecological climax?

What is a beech-maple climax?

In the frontispiece, note the two fine specimens, so large, so handsome, so close together. Have you an adequate explanation? Is there an adequate explanation?

CHAPTER XXII

HEREDITY

We know that bean seeds will give rise to bean plants and that acorns may develop into oak trees. We know also that a bean will produce a bean plant and an acorn an oak tree with as unerring certainty as that night follows day. This is due to the phenomenon known as *heredity*, or that like produces like. However, the aphorism, "like begets like" is true only in a very general way and in special cases. For example, there are hundreds of varieties of apples, yet all apple trees are much alike in certain fundamental respects and all have doubtless been derived from a few wild species. It was also recognized many years ago that there are among beans, peas and other common plants various races or varieties which differ from each other in certain particulars, as in stature, flower color, character of fruits and seeds, etc. Some varieties of peas, for example, have purple, some red, and some white flowers; some are tall, while others are dwarf. In some the seeds are round and smooth, in others they are wrinkled.

For many decades before the time of Mendel, botanists, physicians, and other educated men carried on studies in the hybridization of plants under experimental conditions. Many hybrids were produced and a number of characteristic features, observed in both the first and in the second generation of hybrids, were noted and discussed. Of these features that which we now refer to as dominance, was commented upon by certain of the experimenters. They observed also that numbers of individuals resembled the immediate parents closely, while others resembled one or the other grandparent closely. No very definite rules, however, were formulated which could be applied in a general way.

First among those to be successful in formulating a definite rule in regard to the inheritance of certain distinct characters by the progeny of hybrids, was Gregor Johann Mendel (1822–1884), an Augustinian monk and abbot of Brunn, Austria (now Czechoslovakia). Mendel formulated a principle of heredity which has since become known as *Mendel's Law*,* and which is regarded as one of the most important discoveries of the nineteenth century.

* His paper entitled "Versuche über Pflanzenhybriden," embodying the results of eight years of his own personal experimentation, was published in 1865. It still stands as a classic in the literature on the experimental study of heredity.

Following the idea that such characters as stature, flower color, etc. may be transmitted in hybrid progeny in a definite way, he set out to make experiments, centering his attention upon one set of contrasting characters at a time, in order to observe their behavior from generation to generation. He selected peas, because they were easily cultivated, and because of the fact that, with the aid of greenhouse conditions, two or three crops could be grown in a single year.

One of the first things observed in crossing individuals of two varieties, such as a tall and a dwarf, was that the results were the same no matter which one was taken as the pollen parent or as the ovule parent. In experimental work of this kind, reciprocal crosses are usually made. In any given experiment in case the pollen of the tall plant is used on the stigmas of the dwarf individual or the ovule parent, the reciprocal cross would consist in using the pollen of the dwarf upon the stigma of the tall individual as the ovule parent.

In order to get a clear idea of Mendel's law let us select a simple illustration. A cross is made, let us say, between a tall variety and a dwarf variety of peas. The seeds obtained from the cross are planted and the resulting plants are hybrids, being the offspring of parents of different varieties of organisms. These hybrids constitute the first hybrid generation, or in short the F_1 generation. In these two varieties the set of contrasted characters to be followed was *tallness* and *dwarfness*, one individual possessing tallness and the other dwarfness.

Now, the plants of the F_1 generation are not intermediate in height between the two parents, but they are all tall like the tall parent. They have, however, inherited both dwarfness and tallness, because the fecundated eggs from which they developed contained the germ substance of the two parents, tall and dwarf. But tallness came to expression while dwarfness did not. Dwarfness was hidden or concealed by tallness. We designate tallness, therefore, as the dominant character, and dwarfness as the recessive character.

Plants of the F_1 generation are bred among themselves and seeds secured. From those seeds, plants of the second hybrid, or F_2, generation are grown. Of the entire F_2 progeny it will be found that three-fourths (75%) are tall like the tall grandparent and one-fourth (25%) is dwarf like the dwarf grandparent. In other words there will be approximately three times as many tall plants as dwarf plants, or a ratio of 3 to 1. This is the Mendelian 3 to 1 ratio.

The following diagram will illustrate the foregoing statements (Fig. 541).

The F_1 Generation.—Let us now seek the explanation of the character of the F_1 Generation of plants. In pure strains we say that plants are

tall, because their hereditary substance contains a "factor" or "determiner" (gene) for tallness, but not the factor for dwarfness. Likewise pure strains of dwarf plants contain a "factor" (gene) for dwarfness but not the factor for tallness. The pure strains of tall plants are, therefore, *homozygous* and those of the dwarf plants are also homozygous in regard to the two contrasting hereditary characters, tallness and dwarfness.

Let us represent the expression "factor for tallness" by the capital letter T, and the small letter d for the expression "factor for dwarfness." If a tall plant be pollinized by the pollen of a dwarf variety, in which case

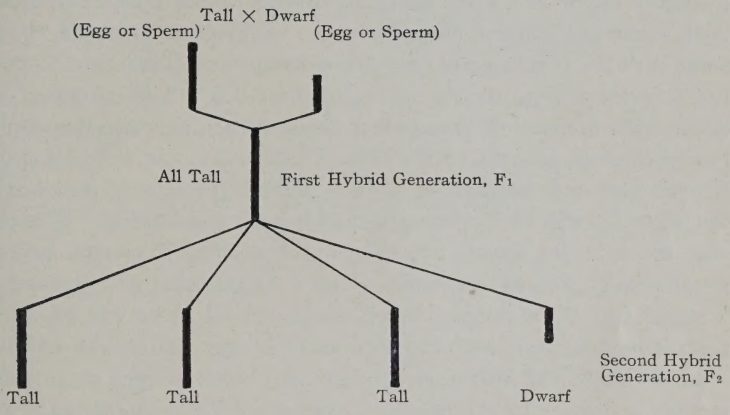


FIG. 541.—Diagram illustrating inheritance in F_1 and F_2 generations in a cross between tall and dwarf peas (Mendelian monohybrid). The F_2 progeny consists of three tall to one dwarf, the 3:1 ratio, or in any progeny however numerous there will be approximately three times as many tall individuals as dwarf individuals.

the T egg unites with the d sperm, a Td zygote results ($T \times d = Td$). Or a dwarf plant may be pollinized with the pollen of a tall plant, in which case the zygote dT will have the same hereditary composition ($d \times T = dT$). The hereditary composition of the F_1 plants will be Td. The F_1 plants are consequently not homozygous but *heterozygous* in regard to the characters tallness and dwarfness, because those plants contain the hereditary substance of both parents. But all are tall like the tall parent. This is because tallness conceals or *dominates* dwarfness. Tallness comes to expression in the F_1 individuals while dwarfness does not. Tallness is referred to as the *dominant* character and dwarfness as the *recessive* character.

The F_2 Generation.—We have noted that all of the plants of the F_1 generation were tall and alike in appearance, but that in the F_2 generation the plants were of two kinds in appearance, tall and dwarf, the ratio being three tall to one dwarf. In order to explain this phenomenon it is neces-

sary to know the hereditary make-up of eggs and sperms produced by the F_1 plants.

We have learned in preceding pages that the pollen mother-cells give rise each to four pollen spores, and that, during the first mitosis in the spore mother-cell, a reduction division took place by which the *number* of chromosomes was reduced to one-half. In this reducing division the chromosomes formed pairs (bivalents). It is assumed that one chromosome of some pair contains the dominant factor *T* in the plant here in question, and that the other chromosome of the same pair contains the recessive factor *d*. The two chromosomes which constitute a pair have been called homologous chromosomes. As division proceeds, the chromosome with the *T* factor will pass to one daughter cell and the one containing the *d* factor will go to the other daughter cell. The daughter cells now divide (the division of the nucleus being equational) and the result is that two of the four pollen spores will be *T* spores and two will be *d* spores. In like manner each megaspore mother-cell will give rise to four megaspores, two of which will be *T* megaspores and two *d* megaspores. It is clear now that the *T* pollen spores will eventually produce *T* sperms, and that the *d* pollen will produce *d* sperms. The *T* megaspores will likewise produce *T* eggs, and the *d* megaspores *d* eggs. In all there will be as many *T* sperms as *d* sperms, and the number of *T* eggs and *d* eggs will be equal. Each F_1 plant will therefore produce two kinds of eggs and two kinds of sperms in regard to the factors *T* and *d*. This phenomenon is known as segregation, or the purification of the gametes. The purity of the gametes is one of the most important features in Mendelian inheritance.

With the chance mating of these gametes the numbers of the different zygotes and their hereditary make-up will be made clear in the following checkerboard diagram. In this diagram the two kinds of eggs are placed in a vertical row at the left, and the two kinds of sperms in a horizontal row above.

Eggs \ Sperms	*T*	*d*
T	*TT*	*Td*
d	*dT*	*dd*

We observe that the combinations are:

T sperm with *T* egg = *TT* zygote
T sperm with *d* egg = *dT* zygote
T egg with *d* sperm = *Td* zygote
d egg with *d* sperm = *dd* zygote.

Inasmuch as three of the four zygotes, and the plants resulting therefrom, contain the factor *T*, these will be tall, while the one *dd* which does not contain the factor *T* will be dwarf. It is clear that the *TT* plants and the *dd* plants are homozygous, and that they represent pure lines. But the *dT* and the *Td* plants are heterozygous or hybrid. It is scarcely possible to distinguish the homozygous or pure dominants from the heterozygous dominants by their appearance. It is necessary to inbreed

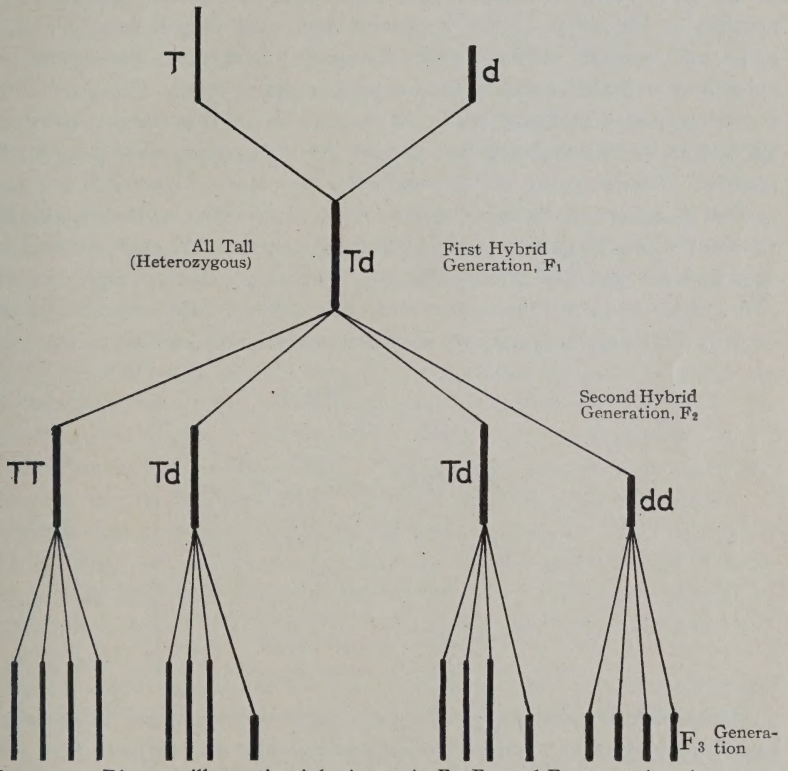


FIG. 542.—Diagram illustrating inheritance in F_1, F_2, and F_3 generations in a cross between tall and dwarf peas (Mendelian monohybrid). All individuals in the F_2 were selfed to give the respective individuals in F_3.

each by pollinizing the stigmas with pollen from the same individual. When this is done pure dominants *TT* will always produce pure *TT* plants, and the *dd* plants will always produce pure *dd* progeny, i.e., they will breed true. On the contrary when the heterozygous plants are inbred their progeny will segregate in the 3:1 ratio. The diagram given above (Fig. 542) will illustrate the inheritance in the F_2 and F_3 generations with reference to the two contrasting characters, tallness and dwarfness.

Dihybrid Crosses.—Plants differing in one set of contrasting characters when crossed will give *monohybrids*. Those discussed in the preceding pages were monohybrids. Mendel was able to make experiments with varieties of peas which differed in two sets of contrasting characters. One of these varieties produced *yellow, wrinkled* seeds and the other *smooth, green* seeds. A cross between two such plants gives *dihybrids*. Since the contrasting characters are seed characteristics instead of those of the adult plant, Mendel was able to judge of the composition of the zygotes in the seeds of the F_1 generation. He found that yellow seed color and smooth surface were dominant characters, while green seed color and wrinkled surface were recessive characters. The development of the spores would not result in two kinds of eggs and two kinds of sperms as in monohybrids but in *four* kinds of eggs and in *four* kinds of sperms. Representing yellow seed color by capital *Y*, smooth surface by capital *S*, green seed color by small *g*, and wrinkled surface by small *w*, the four kinds of gametes will be indicated thus: *YS* eggs, *Yw* eggs, *gS* eggs and *gw* eggs; and *YS* sperms, *Yw* sperms, *gS* sperms, and *gw* sperms. The composition of the zygotes and their approximate proportional numbers in the progeny are shown in the checkerboard diagram:

		Sperms			
		YS	*Yw*	*gS*	*gw*
Eggs	*YS*	*YSYS*	*YwYS*	*gSYS*	*gwYS*
	Yw	*YSYw*	*YwYw*	*gSYw*	*gwYw*
	gS	*YSgS*	*YwgS*	*gSgS*	*gwgS*
	gw	*YSgw*	*Ywgw*	*gSgw*	*gwgw*

Inspection of the diagram shows (1) that one zygote of the sixteen is a pure line dominant *YYSS*, homozygous for color and surface (seed yellow and smooth); (2) one pure line recessive *ggww* homozygous as to both color and surface (seeds green and wrinkled); (3) two zygotes out of sixteen, *YYSw*, homozygous for color and heterozygous for surface (seeds yellow and smooth); (4) two zygotes of the sixteen, *YgSS*, homozygous for surface but heterozygous for color (seeds yellow and smooth); (5) four zygotes of the sixteen, *YgSw*, heterozygous for both color and surface (seeds yellow and smooth); (6) one zygote of the sixteen, *YYww*, homozygous as to both color and surface (seeds yellow and wrinkled); (7) two zygotes of the sixteen, *Ygww*, heterozygous for color and homozygous for surface (seeds yellow and wrinkled); (8) two zygotes of the sixteen, *ggSw*, heterozygous

as to surface and homozygous as to color (seeds smooth and green); (9) one zygote of the sixteen, *ggSS*, homozygous as to color and surface (seeds green and smooth).

If we classify the zygotes as to the appearance of the seeds we shall have the four classes:

(1) 9 yellow smooth
(2) 3 yellow wrinkled
(3) 3 green smooth
(4) 1 green wrinkled

Or the ratio 9:3:3:1

If we consider the two contrasting colors in the progeny we find 12 yellow and 4 green, or the ratio of 3 to 1. The same is true of the two contrasting surface characteristics, namely 12 smooth and 4 wrinkled, or the ratio 3 to 1.

If one operates with plants with three sets of contrasting colors, *trihybrids* will be secured, etc. It is clear that with the larger number of contrasting Mendelian characteristics, the greater will be the number of combinations secured in the hybrids.

Mendel's rule has been of great value in the study of heredity, because it shows definitely how certain hereditary characteristics are transmitted from parents to offspring. It has also enabled the breeder to purify the gametes and to separate the desired strains from the undesired, or to eliminate the undesired altogether. It has shown also what is necessary to keep the undesired eliminated. The rule is applicable in a measure to the human race as well as to plants and lower animals. It is known for example, how such human afflictions as insanity, feeblemindedness, epilepsy, etc. are transmitted in heredity, and it points rather clearly to the procedure necessary in order to eliminate such unfortunates from human society.

However, it is equally important to keep in mind that all hereditary characteristics are not transmitted according to Mendel's law. Sex in plants, for example, is not inherited according to Mendelian ratios. *There are no sex chromosomes in plants.* The most direct and reliable experimental evidence goes to show that sex is *quantitative* and not *qualitative.* Every plant sporophyte or diploid structure is potentially bisexual, because it has originated from the union of male and female gametes. Some sporophytes, however, will produce only male reproductive cells or only functionally male cells, while others will produce only functionally female reproductive cells. Such diploid structures are said to be functionally unisexual or dioecious. That is, one individual brings to functional expression maleness, and the other individual develops functional femaleness.

When we speak of sex control in plants we merely refer to a method of culture which will bring to expression in dioecious, though potentially bisexual, sporophytes either maleness or femaleness. The Jack-in-the-pulpit (*Arisaema triphyllum*) among others* is a classical illustration. If corms are taken at the proper time and grown with suitable water supply and with the application of an abundance of fertilizer, they will develop ovulate plants. On the contrary, lack of copious nourishment will lead to the development of staminate plants from the same corms. Maleness or femaleness is not changed by the experimental treatment. Such treatment merely gave opportunity for one or the other sex potentiality to come to expression.

The experimental study of heredity by means of hybridization has been one of the most important factors in shaping recent biological thought. Through hybridization a wide range of modifications and combinations is brought into existence, and the adjustments of these modifications to the environment through long periods of time have contributed largely to that progressive development which has culminated in the diversified organisms of the past and of those existing at the present time.

* Sex reversal is known to be due to the attacks of parasitic fungi and to other causes.

INDEX

Black numbers refer to illustrations

Abies, 428, 564
Abieteae, 565
Absorption of water, 156
Acacia, 316, **534,** 562
Achene, **522,** 523
Achlya, **294**
Acorn, **526**
Actaea, **490**
Adiantum, 112, **113,** 186, 385
Aecidiospore, 316
Aeciospore, 316
Aerobic bacteria, 200
Aesculus, 78
Agaricus (see Psalliota), **325**
Agropyron, 561
Ailanthus, **534**
Air, composition of, 48
Akinete, 238
Albugo, 287, **288, 289, 291, 292**
Alcohol, 172
Alcoholic fermentation, 296
Aleurone, 15, **58**
Algae, blue-green, 194
Alisma, 555
Althea, **505**
Amblystegium, **369**
Ambrosia, 538
Aminita, **334**
Amino-compound, 55
Ampelopsis (see Psedera)
Amphiora, 271
Amphiphloic siphonostele, **136**
Anabaena, **196**
Anabolism, 54
Andraecium, 473, 502
Andreaeales, 378
Androspore, 243, 244
Angiopteris, 399
Angiosperms, 470
Annual rings, **98, 99, 100**
Annulus, 385, **386**
Anther, **473, 474, 475**
Antheridiophore, **350, 366, 368, 374**
Antheridium, 343, **352,** 370, 371
Anthoceros, 354, **357,** 358, **359,** 362, 363
Anthocerotaceae, 358
Anthocerotae, 353
Anthocyanin, 13, 74
Antipodal cells, **477**
Aplanospore, 207, 238
Apogamy, 397, 484
Apophysis, **375, 376**
Apospory, 397
Apothecium, 304
Arbor-vitae, 428
Archegoniophore, **349, 366,** 367, **368, 374**
Archegonium
  in gymnosperms, **441, 442**
  in Hepaticeae, **343, 351**
  in Musci, **372**
  in Pteridophyta, 389, **391**
Arctium, **536**
Arctostaphylos, 566
Ardisia, 204
Aril, 165
Arisaema, **497,** 576
Aristolochia, **95,** 97
Arnica, **507, 508**
Artemisia, 547
Arthrospore, 200
Ascent of sap, 159
Ascogonous filaments, 305
Ascomycetes, 296
Ascophyllum, 264
Ascus, 295, **304**
Ash constituents, 55
Asparagus, 120, 566
Aspergillus, **300**
Aspidium, 383, **384**
Asplenium, 398
Autonomic movement, 184
Autumnal coloration, 74

Auxospore, **221,** 222
Azolla, 398, 406

Bacillariales, 215
Bacillus, 203
Bacteria, 198, **199,** 200
  iron, 201
  nitrifying, 201
  nitrogen-fixing, 201
  pathogenic, 203
  sulphur, 201
Bacterio-purpurin, 201
Bacterium aceti, 172, 173
Bald cypress, **147,** 450
Balsam, 59
Barberry, **319, 320**
Bark, **98, 105**
Basidiomycetes, 312
Basidium, **312, 328**
Batrachospermum, 271, **272, 273, 274**
  juvenile form, **275**
Bean, Lima, **2**
Beggiotoa, 201
Bennettitales, 450, 452
Berberis (Barberry), 319, 320
Berry, 524
Betula, 503
Bidens, **536**
Bignonia, **535**
Bird's nest fungus, 332, **333**
Black knot of plum, **301**
Black leg of potato, 204
Black walnut (see Juglans)
Blackberry, **525**
Blastophaga, 520
Blepharoplast, **390**
Blue-green algae, 194
Bog, 557
Bole of tree, 109
Boletus, **331,** 332
Border parenchyma, **46**
Bordered pits, **107, 108**
Botrychium, **400, 401**
Botrydium, 250, **251**
Bouteloua, 543
Brown snow, 552
Bryales, 378, 379
Bryonia, **65, 66**
Bryophyllum, 72, **73,** 201
Bryophyta, 188, 339
Bryopsis, **251**
Buchloe, 543
Budding in grafting, **122**
Budding in yeast, **296**
Buds, 1, 2, **79, 80**
  cotyledonary, 4
Bulb, bulbil, bulblet, 118, **119, 471**
Bulgaria, 304
Butternut, bud of, 81
Buxbaumia, **376,** 378

Cabbage, club root of, 193
Cactus, **544, 545, 546, 549**
Caeoma, 323
Calamovilfa, 561
Calluna, 557
Calyptra, **364**
Calyx, 471
Cambium, 86, 87, **95, 96, 97,** 99
  fascicular, 86, 88
  interfascicular, 86, 88
  origin of rays from, 97
  origin of wood and bast from, 97
Camphor, 59
Camptosorus, **73**
Canna, **508**
Caoutchouc, 59
Capillitium, 192
Capsella, 288, 289, **472, 473, 486**
Capsule, **364, 375**
Carinal canal, **410**
Carotin, 12
Carpel, 428, 430, 470, 472
Carpinus, 502
Carrot, 143
Carya, **79**
Caryopsis, 522
Castalia, 500, **504,** 554
Catharinea, **377,** 378
Catkin, 461, **497**
"Cedar apple" (cedar gall), 222, **323**
"Cedar berry," 450, **451**
Celastrus, 576
Cell, **7, 8, 9, 10**
Cell division,
    by cell plate, **24**
    by cleavage furrows, 25, **26**
    by constriction, **24, 25**
    by free cell formation, **27**
Cell inclusions, 16
Cell plate, **24**
Cell sap, 8

Cell wall, **7, 9, 10**
Cellulose, 29
Cerastium, 524
Ceratophyllum, 552
Cereus, 547, **549**
Cetraria, 549
Chaetoceros, 218
Chaetophora, 239
Chalaza, **163, 164, 476, 486**
Chapparal, 547
Chara, 252, **253, 254, 255, 256,** 257, 555
Charales (Charophyta) 252
Chasmophyte, 558
Chemosynthesis, 201
Chemotaxis, 183
Chemotropism, 183
Chlamydomonas, **232,** 233
Chlamydospore, 314
Chlorella, 226
Chlorenchyma, **87**
Chlorococcum, 225
Chloroplast, **7, 10**
Chlorophyll, 12
Chondrioderma, 192
Chondriosomes, **9**
Chondromyces, 204
Chromatin, 10
Chromatin reticulum, **491**
Chromatin spirem, **491**
Chromoplast, 10, **16**
Chromosomes, **23**
  bivalent, **492**
Crootheca, 195
Chytridiales, 295
Cinchona, 104
Cladodium, 120, 408
Cladonia, **309,** 549
Cladophora, 235, **236, 237**
Cladothrix, 201
Clamp connections, **329**
Clavaria, 329, **330**
Claviceps, 300, **301, 302**
Claytonia, 576
Cleistogamous flowers, **514**
Climacium, 378
Closterium, **213, 214, 216, 250**
Coal plants, 423
Coconeis, 221
Coconut, **532**
Codium, **251**
Coenocyte, 10
Coleorhiza, **166**
Columella
  in liverworts, **357, 359**
  in mosses, **375**
  in Rhizopus, **284**
  in slime moulds, 191
Companium cells, **89**
Compass plant, 38, **39**
Conceptacle, **261**
Conduction of water, 159
Conferva, 238
Confervoideae, 235
Conidia, **298**
Conidiophore, **298**
Coniferales, 235, 450, 461, 466
Conjugales, 206
Connecting fibers, 23
Connective, **473**
Conocephalus, **355**
Conopholis, 155
Coprinus, 330
Cora, 306
Corallina, 271
Cordaitales, 450
Cordaites, **422**
Cordyceps, 302, **303**
Corispermum, 561, 563
Cork, 102, 104
Corm, **119**
Cornus, 561, 562, 576
Corolla, 471
Cortex, primary, 91
  secondary (see phelloderm)
Corymb, **572**
Cosmarium, **213, 216**
Cosmos, **506**
Cotton boll, 533
Cotyledon, **1**
Crocus, 119
Cromatium, 201
Cronartium, 323
Crown gall, 202
Crown root, 144
Crucibulum, **332**
Cryoplankton, 552
Cryptostoma, **266**
Crystalloid, 18, **19**
Cucumber wilt, 203
Cucurbita, 203
  sieve tube of, **89**
Cup fungus, 303, **304**

Cupresseae, 565
Cutin, 42
Cyanophyceae, 194
Cyathus, 332
Cycadales, 455, 466, 467
Cycadeoidea, 452, **453**
Cycadinocarpus, 459
Cycadofilicales, 450, **451**
Cycas, 456
Cylindrospermum, 197
Cymbella, 218
Cyme, cymose, **511**
Cypress swamp, 558
Cystocarp, 274
Cystopteris, 397
Cystosporeae, 259
Cytoplasm, 7
  connections between cells, **27**, 28
  movement of, 8

Dahlia, 144
Dandelion, 142
Delphinium, 476, 477, **479**
Dendroceros, 358
Dentaria, 576
Desmids, **213, 214,** 215, **216**
  movements of, 223
Desmodium, 536
Diastase, 171
Diatomaceous earth, 223
Diatomin, 218
Diatoms, 215, 216, **217, 218, 219, 220, 221, 222**
  movement of, 223
Dicentra, 576
Dicksonia, 111
Diclinous flowers, 498
Dictyophora, **333**
Dictyostele, 136
Dictyota, **269, 270**
Dictyotales, 268
Diffusion, 136
Digestion, 171
Dihybrid, 586
Dioecious, 286, 499
Dionaea, 70, **71**
Diploid structure, 210
Dispersal of plants, 537
Docidium, 213
Dorycordaites, 457
Draparnaldia, **239**
Drosera, **69**
Drupe, 524
Dryopteris, 283
Dunes, 560
Dwarf male, **243**

Earthstar, **332**
Ecballium, **531**
Ectocarpus, **265, 266**
Ectophloic siphonostele, 136
Egg, 5, **477**
Egg-apparatus, **477**
Egregia, 267
Eichornia, 550
Elaeagnus, **44**
Elater, **191, 342, 408**
Elm, 105
Elodea, **7,** 9
Elymus, 561
Embryo
  of dicotylous plant, **484, 485**
  of monocotylous plant, **487**
  of Pinus, **431, 446**
  of Tsuga, **445**
Embryonal path, 444
Embryo-sac, **477**
Empusa, 295
Emulsion, 18
Endodermis, **85, 87**
Endosperm, 440, **441, 442, 445**
  development in Angiosperms, 486, 488
  Gymnosperms, 440
Endosperm cell, primary, **477, 483**
Endospore, 386
Endothecium, **475**
Enteromorpha, 240
Entomophthora, 295
Entomophthorales, 295
Enzymes, 171
Ephedra, 428, **462,** 463, 466
Epicarp, 522
Epicotyl, **1, 166, 168**
Epidermal hairs, **43, 44, 45**
Epidermis, 40, **41**
Epifagus, 154
Epinasty, 184
Epiphragm, **376**
Epiphyte, **572**
Epithema, **62**
Equisetineae, 383, 397, 398, 406

Equisetum, **407, 408, 409, 411**
Ergot, 300, **301**
Erysiphe, 298
Erythronium, 576
Etiolin, 13
Eumycetes, 282, 295
Eusporangiate ferns, 398
Exine, **434**
Exospore, 386
Exudation of water, 62

Fagus, **498**
Fairy ring, 329
Fecundation (fertilization)
in ferm, **392**
in Lilium, **482**
in Pinus, **444**
in Spirogyra, **207**
Fegatella (Conocephalus), **355**
Fermentation, 296
Fertilization (see fecundation)
Festuca, **510**
Fibers, **90**
Ficus, 573
Fig, **520,** 526
Fig wasp, **520**
Filament, **5, 473**
Filices, 398
Filicinae, 383
Fimbriaria, 353
Flax, retting of, 29
Floral leaves, 471
Flowers
of Angiosperms, **4, 471,** 498
of Ephedra, **462**
of Ginkgo, **460**
of Gnetum, **463, 464**
of Pinus, **431**
of Tulipa, **471**
of Welwitschia, **465**
opening and closing of, 184
Flowers, kinds of,
cleistogamous, **512,** 514
diclinous, 498
epigynous, **503**
hypogynous, 503
monoclinous, 498
of Compositae, 504, **506, 507, 508**
of grasses, **409, 410**
pistilate, 498
polypetalous, 501
Flowers, kinds of, staminate, 498
sympetalous, 501
Fly mould, 295
Foam, 18
Foliar gap, 112, **113**
Follicle, 522
Fomes, 332
Food storage, 56, 57
Forests
deciduous dicotylous, 573
evergreen, coniferous, 565
evergreen, dicotylous, 571
mesophytic, 571
of eastern U. S. 540
of Pacific slope, 541
of Rocky Mts., 541
tropical, rain, 571, 572
Fructose, 172
Fruit, **5,** 488, 521
aggregate and accessory, **525**
dispersal of, 529
dry dehiscent, 523
dry indehiscent, **522**
formation in Angiosperms, 521, 522
of fig, **526**
seedless, 526
succulent indehiscent, 524
Frullania, 353
Fucales, 259
Fucoxanthin, 13, 259
Fucus, 259, **260, 261, 262, 263**
Fuligo, 188, **189**
Funaria, **364, 365, 366, 367, 368, 370, 371,** 374, 375
Function of phloem, 158
of xylem, 158
Fungi, 282
Fungi cultivated by ants, 334
Fungi Imperfecti, 295
Funiculus, 476, 486

Gallionella, 201
Gamete, 207
Gametophyte, 339
Geaster, 332
Gel, 18
Gemmae, **346,** 347, 348, **350**
underground, **366**
Gene, 583
Geotropism, 181, **182**
Gill of mushroom, **327**

Ginkgo, 428, **460,** 461, 466
Ginkgoales, 450, 459, 467
Gladiolus, **119**
Glands, **43**
Glaucocystis, 195
Gloeocapsa, 194, **195,** 196, 552
Glucose, 172
Gnetales, 450, 462
Gnetum, 428, **463, 464,** 466
Gomphonema, **218**
Goodyera, 566
Grafting, **121, 122, 127**
Grapefruit, 524
Grassland, 542
Grass-Steppe, 542, 543
Green snow, 552
Growth, 177
  by accretion, 177, 180
  by hydration, 177, 179
  embryonic, 177
  work done by, 180
Gymnoconia, 323
Gymnosperms, 428, 470
Gymnosporangium, 321, 324
Gynoecium, 473, 503
Gypsophila, 543

Haematococcus, 233, 552
Halimeda, 251
Halydris, 264
Hamamelis, 530, **531**
Haploid structure, 210
Haustoria, 293
Haw, hawthorn, 322
Healing of wounds, 105, 249
Heartwood, 108
Helianthemum, 568
Helophyte, 553
Hemiascineae, 296
Hemicellulose, 29, 57
Hemitrichia, **189, 191**
Hepatica, 576
Hepaticeae, 353
Heredity, 581
Heterocyst, **195,** 196
Heterosporous Pteridophyta, 398
Heterotypic mitosis, 490
Heterozygous, 583
Heuchera, 559
Hickory, **79**
Holcus, **476**
Homeotypic mitosis, 496
Homozygous, 583
Hordeum, 545
Hormogonia, 198
Horse-chestnut, 78
Hottonia, 550
Houstonia, 518
Hydatode, 52
Hydnum, **331,** 332
Hydrangea, 559
Hydrocharis, 552
Hydrodictyon, 226, **227, 228, 229,** 230
Hydrophyte, 212, 550
Hydrotropism, 183
Hymenium, **328**
Hyoscyamus, 473
Hypnum, 378
Hypocotyl, **1**
Hypocynus, 328
Hyponasty, 194

Imbibition, 137
Impatiens, 530
Inarching, 123
Inclusions, 16
Indian pipe, 152
Indian turnip, 497, 512, 596
Indusium, **384, 385**
  false, 385
Inflorescence, 511
Insectivorous plants, 69
Integument, **437, 481**
Intine, **434**
Inulin, 144
Invertase, 172
Iris, 36, **522**
Isoetaceae, 421
Isoetes, **422**

Jack-in-the-pulpit, **497,** 512, 596
Jeffersonia, **522,** 537
Juglans, **501,** 547
Jungermanniaceae, 356
Juniperus (Juniper) **321, 324,** 428, **451,** 462, 564, 566
Jussiaea, **148,** 550
Juvenile leaf, 1

Kaolin, 201
Karyogamy, 193
Katabolism, 174

Kieselghur, 223
Knot, 109

Lachnea, 27
Laminaria, 267, 268
Larix, 428, 458
Larkspur, **476, 477,** 478
Latex, 92
Latex tube, vessel, **90, 92**
Lathyrus, 530
Layering, 123
Leaf, 31
  arrangement on stem, 36, **37**
  day and night position, **39**
  drip tip of, **573**
  epidermis of, 40, **41**
  equitant, 36
  fall of, **78**
  food storage in, 74
  forms of lamina, **35, 36, 37**
  function, 46
  horizontal position, 38
  internal surface, **41,** 45
  light position of, **38**
  mesophyll of, **41,** 44
  of Ephedra, **463**
  of fern, **384**
  of Ginkgo, **460**
  of Gnetum, **464**
  of Juniperus, **451**
  of Pinus, **448, 449**
  of Thuja, **450**
  of Welwitschia, 464
  origin and growth, **39,** 40
  petiole of, **32, 33, 34,** 46
  primordia, **40**
  stomata, **41**
  structure, **41**
  venation, **32,** 33
Leaf trace bundle, 92
Lecanora, 312
Legume, **522, 530**
Leguminous tubercle, **149,** 151
Lejeunia, 353
Lemanea, 276
  juvenile form of, **277**
Lemna, 550
Lemon, 523
Lenticels, 74, 103, **104**
Leptosporangiate ferns, 398
Leptothrix, 201
Leuconostoc, **9**
Leucoplasts, **13, 15**
  origin of, **14**
  relation to chloroplasts, 14
Lichens, 305, 306, **307, 308**
Licmorpha, **218**
Lignin, 88
Ligule, **34,** 420, **422**
Lilium, 476, 480, 481, **484,** 545
Lily-of-the-valley, 512
Linaria, 182
Linden, **99, 100,** 102, **535**
Lipase, 172
Lithophyte, 558
Liverwort, 339
Llanos, 542
Loculicidal, 522
Lumber, clear, 109
Lunularia, 353, 355
Lupulin, 43
Lycogola, 188, **189**
Lycoperdon, 331, 332
Lycopodiaceae, 411
Lycopodineae, 383, 397, 411
Lycopodium, **411, 412, 415**
Lysimachia, 556
Lythrum, 518

Macrocystis, 259
Magnolia, 455
Maidenhair fern, **112, 385**
Malva, **513,** 514
Maple, bud of, **81**
Marl, 258
Marattia, 399
Marchantia, **11, 346,** 347, **348, 349, 350, 351,** 353
Marchantiaceae, 353, 355
Marsilia, **402,** 403
Marsh plants, 553
Marsiliaceae, 403
Martynia, 536
Matteuccia (Onoclea) 386, **394**
Meadow, 570
Medicago, 545
Medulla (Pith), 94
Megagametophyte, **441, 442,** 477, **478, 479,** 480
Megasporangium, 403
Megaspore, **438,** 478

Megaspore mother-cell, **437, 476, 478,** 481
Megasporophyll, **404,** 431
Melilotus, 85
Melosira, 221
Mendel's law, 581
Merismopedia, 197
Meristem
  ground, 93
  primary, 93
  primordial, 93
Mesocarp, 522
Mesocarpus, 212
Mesophyll, 44
Mesophyte, 212, 566
Metabolism, 54
Metzgeria, 353
Micrasterias, **213**
Micrococcus, **199**
Microgametophyte, **404,** 442, **443,** 481
Micropyle, **431, 435, 436, 437, 438**
Microsphaera, 297
Microsporangium, 403
Microspore, 433, **434**
Microsporophyll, 431, **434,** 471
Middle lamella, 28
Mildew, 297
  downy, 294
  powdery, 297
Mimosa, 67, **68**
Mitochondria, **9**
Mitosis, **21, 22,** 490
Mnium, 378
Monoclinous flower, 498
Monoecious, 286, 499
Monohybrid, 584
Monotropa, **152**
Moor, 557
Morchella, 305, **306**
Morel, 305, **306**
Mosses, 364
Mougeotia, 212
Mould
  black, 299
  blue, 299
  bread, 283
  water, 294
Movement, autonomic, 184
  of food and water, 157
Mucorales, 295
Mulberry, 525
Munroa, 543
Musci, 364
Mushroom, 325
Mycelia Sterilia, 295
Mycomycetes, 186, 188, 282, 295
Mycorhiza, **149**
Myxamoeba, **182, 183**
Myxobacteriaceae, 204
Myxomycetes, 186

Nasturtium, 4, **5, 32,** 51, **63**
Negative gas pressure, 161
Nelumbium, **532**
Nepenthes, **90**
Nephrolepis, **385**
Neutral line, 20
Nitella, 258
Nitrifying bacteria, 201
Nitrobacter, 201
Nitrogen-fixing bacteria, 201
Nitrosomonas, 201
Node, 77
Nodule forming bacteria, 149, **150,** 201
Nostoc, **195,** 196, **310**
Notothylas, **357, 360, 361, 362**
Nucellus, 437
Nuclear membrane, 10
Nucleolus, **9**
Nucleus, **7, 9**
  direct division of, 21
  equational division of, 23
  indirect division of, 23
  reducing division of, 210, **211,** 490
Nut, 525, **532**

Oedogonium, **240, 241,** 242, **243,** 244
Oil, 54, 58
  aromatic, 58
  castor, 54
  essential, 58
  linseed, 54
  olive, 54
  peanut, 54
Onoclea, 386
Oögonium, 242, **243**
Operculum, 365, **400**
Ophioglossaceae, 399
Ophioglossum, 363
Opuntia, 538
Orange, 523
Orchis, 509
Oscillatoria, **195,** 196

Osmosis, 137
Osmotic pressure, 137
Osmunda, 402
Osmundaceae, 410
Ovulary (ovary), 472
Ovulate strobilus (cone), 433
Ovule, 477, **478**
Oxalis, 531
Oxalophyte, 556
Oxidase, 172, 173

Paeonia (Peony), 305
Palea, 409, **410**
Pallavacinia, 353
Pampas, 542, 544
Pandorina, 229, 230, **231**
Panicle, 511, **512**
Paraphyses, **304, 307, 328, 370**
Parenchyma, 88
Parmelia, 308
Parthenocarpy, 526
Parthenogenesis, 537
Pathogenic bacteria, 203
Peat, 143, 557
Peat moss, 378, **379, 380**
Pecopteris, **452**
Pectin, 29
Pectose, 29
Pediastrum, **225,** 226
Pellaea, 558
Pellia, 353, **356**
Penicillium, 300
Pepo, 524
Perianth, 471
Periblem, **128, 135**
Pericarp, 522
Pericycle, 86, 94
Perigone, 471
Perinium, 386
Peristome, 365, 375
Perithecium, 299
Peronosporales, 295
Petals, 471
Petiole, 31, **32, 33**
Petiole, anatomy of, 46
Peziza, 303
Phaeophyceae, 259
Phaeosporales, 265
Phajus, 15
Phase, disperse, continuous, 18
Phaseolus, 163
Phelloderm, 102
Phellogen, 102
Phloem, 158
Photosynthesis, 46, 47, 48
Phototaxis, 182
Phototropism, 182
Phragmidium, 320
Phycocynanin, 13
Phycoerythrin, 13, 271
Phycomycetes, 282, 295
Phycophaein, 13
Phyllactinia, 297
Phyllodium, **66,** 67
Phylloglossum, 413, **416**
Phyllosiphon, 252
Physcia, 306, **307**
Phytophthora, 294
Picea, 428, 541
Pileus, 325
Pilobolus, **26, 286, 287**
Pilularia, 398, **405**
Pinaceae, 461, 462
Pine tree moss, 378
Pinnularia, **217, 219, 220**
Pinus, 11, 96, 106, 178, 428, **435, 436, 437, 438, 439,** 440, **441, 442,** 446, 541, 562
  bordered pits in, **107, 108**
  cambium, **96**
  cone, **430, 432,** 433
  flowers of, 431, **432, 433**
  germination of seed, 447
  pollen, 434
  seed, germination of, 447
  torus, **108**
  xylem in perspective, 107
Pistil, **5,** 428, 470, **472,** 483
Pisum, 9
Pitch, 82, 86
Pits, 28
Placenta, 476
Planktionella, 218
Plasma membrane, 10
Plasmodesmi, 28
Plasmodiophora, 193
Plasmodium, 188, **190**
Plasmolysis, 139
Plasmopora, 293, 294
Plastid primordia, 11, **12**
Plastids, 8, 10
Plerome, **128, 135**

Pleurococcus, 224
Pleurosigma, **218**
Plowrightia, 300, **301**
Podocarpus, 461
Podophyllum, 576
Pollen, development of
in Angiosperms, 489
in Pinus, 434
Pollen mother-cell, 490
Pollen spore, **475, 495**
Pollen tube, 5, **482, 483**
Pollination (pollinization)
in Angiosperms, 513
in Pinus, 436
Polyganum, 556
Polygonatum, **32, 33**
Polyhedron, 230
Polypodiaceae, 398
Polypodium, 398
Polysiphonia, 278
Polystele, **114,** 116
Polytrichum, **376,** 378
Pome, 524
Pontederia, 555
Poppy, 524
Populus, 561
Porella, 339, **340, 341, 342, 344, 346,** 353
Potato, powdery scab of, 194
Potato tuber, 121
Potentilla, 505
Prairie, 542
Prickle, **117**
Primary meristem, 93
Primary rays, 94
Primordial meristem, 93
Primordial utricle, 9
Primula, **62**
Procambial strands, 93
Proembryo, **257, 445,** 446
Promycelium, 317
Propagation
by spores, 192, 195
vegetative, 123, 197, 200
Protease, 172
Prothallium, 386
Protococcus, 224, **225**
Protoderm, 93
Protonema, primary, 365
secondary, **366**
Protophloem, **83**
Protoplasm, 16
colloidal character of, 17
Protoplasmic movement, 20
amoeboid, 21
ciliary, 21
effect of temperature upon, 21
rotary, 20
streaming, 20
Protosiphon, 250
Protostele, 136
Protoxylem, 84, 86
Prunus, 505, 561
Psalliota (Agaricus), 325, **326,** 329
Psammophyte, 559
Pseudoparenchyma, 327
Pseudopodium, **378**
Pseudotsuga, 428, 541
Psilotaceae, 413
Ptelea, 534
Pteridophyta, 188, 467, 423, 424
Pteris (Pteridium), 113, **114,** 566
Puccinia, 316, **317,** 320
Pulvinus, 67
Pumpkin seedling, 169
Pycnia, 319, **320**
Pycniospores, 319, 320
Pyrenoid, **201**
Pyronema, 303, **305**
Pyrus (apple) 305
Pythium, 294

Quercus, 109, **500,** 564

Raceme, 511, **512**
Rafflesia, 154
Rapistrum, 543
Rays, medullary, 94, **96, 99**
origin from cambium, 97
primary, 94
secondary, **100**
Reboulia, 356
Red snow, 552
Reducing division, 490, **491, 493**
Reed swamp, 555
Resin duct, 106, **449**
Respiration, 171, 174
Response to stimuli, 180
Reticulum, 24
Rheotropism, 183
Rhizine, 306

Rhizoid, **247, 253, 341, 346, 366, 388**
Rhizome, **119**
Rhizopus, **283, 284, 285**
Rhodobryum, 378
Rhodophyceae, 271
Rhopalodia, 222
Rhus, 576
Riccia, 353, **354**
Ricciaceae, 353, 354
Ricciocarpus, 353, **354, 355**
Ricinus, **58, 164, 165,** 530
Rivularia, 195, **197**
Robinia, 109
Rochella, 312
Root, **2, 126, 127, 128**
adventitious, 2, 143
aerating, **146,** 147
aerial, **148**
anomalous thickening of, 133
buttress, **145**
clinging, 145, **146**
contraction of, 180
crown, **143**
fibrous, 2, **120**
growing point, **128, 135**
of fern, 135
of parasites, **153, 154**
origin of root branches, **131, 132**
pressure, 160
primary, **1, 143**
prop, 145, **146**
secondary, **2, 143**
secondary, thickening of, 131, **133**
stilt, 145
structure of, 131, **133**
tap root, **142**
tuberous, **144**
Root cap, **128, 135**
Root pressure, 160
Rozites, 335
Rubber, (caoutchouc) 59
Runner, 120
Rusts, 315
black stem, **316**
cedar, apple tree, 322, **323, 324**
methods of control, 324
pine, 323
red, 316, 317
wheat, **317,** 318, 319
"white," 287
Saccharomyces, 172, **296**
Sachs' phases of growth, 177
Sagittaria, **287**
Salicornia, 556
Salix, **497,** 561
Salvia, **516, 517**
Salvinia, **406,** 552
Salviniaceae, 403
Samara, 522, **534**
Sambucus, 123
Sand plants, 559
Sanguinaria, 537, 576
Sap, ascent of, 159
Sap wood, 108
Saprolegnia, 295
Saprolegniales, 295
Sargassum, **264**
Sarracenia, 69, **70**
Sauriana, 532
Savannah, 547
Saxafraga, 558
Scenedesmus, **224**
Schizocarp, 522
Schizomycetes, 194, 198
Schizophyta, 187, 188
Schizosaccharomyces, 297
Sclerenchyma, 84, 87
Sclerotium of ergot, **301, 302**
of slime mould, 191
Secondary tissue, 94
Sedge, 511
Sedum, 558
Seedling of corn (Zea) **168**
of Lima bean, **1, 168**
of pea, **168**
of pumpkin, squash, **169**
of Ricinus, **164, 165**
Seeds, 163, **164, 165, 166,** 485, 488
Selaginella, 414, 416, **417, 418, 420**
Selaginellaceae, 414, 572
Self-plasmolysis, 208
Sensitive plant, **67**
Sepals, 471
Septicidal, 524
Sequoia, 428
Seta, **352, 364**
Sheath, 34
Shepherd's Purse (see Capsella)
Sieve tube, 84, 87, **89**
Silene, 576
Silenium, oxidizing of, 201

Silique or silicle, 523
Siphonales, 246
Siphonastele, **111,** 136
Smuts, **313,** 314, 315
Soil, 140, 141
Sol, 18
Solanum, 121
Solomon's Seal, **33**
Solute, 18
Solution, 18
Solvent, 18
Soredia, 310
Sorus, **384, 385**
Spadix, 497, 512
Spathe, **497,** 512
Spectrum, 49
Sperm, 5, **233**
Spermatium, **310**
Spermatophyta, 188, 428, 470
Sphaerella, 233
Sphaerotheca, 298
Sphagnales, 378
Sphagnum, 378, **379, 380**
Spike, 511
Spikelet, **509, 510**
Spindle, bipolar, **22, 493**
multipolar, 493, 494
Spindle fibers, **22, 493**
Spine, 63
Spirem, chromatin, **23, 492**
Spirillum, **199**
Spirochaete, **199**
Spirogyra, 206, **207**
Spongospora, 194
Spongy tissue, **41,** 44
Sporangiophore, **289**
Sporangium, 284, **289, 386, 387, 396,** 411
Spore, definition of, 198
Spore tetrad, 495
Sporocarp, **402, 406**
Sporodinia, **26**
Sporophylls, **402, 407, 408**
Sporophyte, 339
Squirting cucumber, 531
Stamen, **474**
Staminate flowers, **432, 498**
Staminate strobilus, **432, 462**
Starch, **56, 57, 58**
Starch sheath (endodermis), 88
Staurastrum, 213
Stele, 135
Stem, 77, 91, 93, 98, **100, 101**
anatomy of 81, 82
annual biennial, perennial, 116
dicotylous, 77, 84
monocotylous, 82, 109
of fern, 111
of Pinus, **106**
origin of tissues in, 93
secondary thickening of, 94, 100
twining, 116
Stemonitis, **189, 191**
Stigeoclonium, 239
Stigma, 312
Stink horn, **334**
Stipules, 31, **32, 33**
Stolon, 120
Stomata, 41, 86
Stomium, 475
Stone-fruit, 524
Stony cells, 87
Strand plants, 560
Strawberry, 525
Strobilus, **430, 433**
Style, **5, 472, 482, 483**
Stylophorum, 537, 576
Suberin, 102
Suspension, 18
Suspensor, **420, 445, 446, 485, 486, 487**
Symbiosis, 149, 151, 309
Synangium, 401, 455
Synergids, **477, 484**

Tabellaria, 218
Tamarack swamp, 558
Tap root, 142
Taraxicum, 506, **533**
Taxaceae, 461
Taxodium, 428, 558
Taxus, 428, 461
Teleutospore, 316
Telia, 316, **317, 319**
Teliospore, 317, 318, 319
Tendril, leaf, **33, 63**
stem, **65,** 116
Testa, 165
Thallophyta, 187
Thigmotropism, 182
Thiocystis, 201
Thorn, **117,** 118
Thuja, 428, **450,** 564
Tilia, **99, 101,** 535

Tilletia, **314**
Tomato, 524
Torus, **108**
Touch-me-not, 530
Tracheal tube, 84, 88
Tracheids, 83, 89, 90, 115
Tradescantia, 8
Trama, 328
Transpiration, 46, **59,** 160
Traumatropism, 182
Trichodesmium, 194
Trichogyne, **272, 273, 310, 311**
Tropaeolum (Nasturtium), 4, **5, 32,** 51, **63**
Truffle, 305
Tsuga, 428, **445,** 541, 562
Tuber, 120, **121**
Tubercle, 149
Tuberous, root, 144
Tulip tree, 65, 576
Tulipa, 470, **471,** 472
Tumboa (Welwitschia), **464, 465**
Tundra, 548
Turgor, 140
  movements due to, 67
Tyloses, 109

Ulmus, 504
Ulothrix, 238
Ulva, 240
Umbel, 512
Uncinula, 297
Uredinales, 315
Urediniospore, 317
Uredospore, 317
Urnula, **304**
Urtica, 44
Usnea, **309**
Ustilago, **313**
Ustiliginales, **313**
Utricularia, 70, **72,** 552

Vacuole, 8, **9**
  pulsating, 21
Vallecular canal, **410**
Vallisneria, **515, 551**
Vascular bundle, 82
  bicollateral, 92
Vascular bundle, cauline, 92
  collateral, 92
  concentric, 112
  course, of, 92
  leaf trace, **92,** 113
  radial, 129
Vaucheria, 246, **247,** 248, **249, 250**
Vegetable ivory, 29
Venus fly-trap, **71**
Vessel, 87
  annular, 84
  latex, **90, 92**
  pitted, 87
  reticulated, **90**
  spiral, 84, **87**
Vicia faba, **150, 179**
Viola (violet) 513, **530**
Volvocales, 229
Volvox, **232, 234**

Walking fern, **73**
Water gland, **62**
Water mould, **294**
Water table, 142
Wax, **43**
Welwitschia, 462, **464, 465**
Willow, black, **297**

Xanthium, **536**
Xanthophyll, 12
Xenia, 483
Xerophyte, 212, 558
Xylem, 83, **85, 87, 91, 95, 98, 100, 106, 108,** 112, 114

Yeast, **296**
Yucca, **519, 548**

Zamia, **454, 455**
Zea, **34, 82, 110,** 111
Zoöglea, **199**
Zygnema, 212
Zygnemaceae, 212
Zygophyceae, 206
Zygote, 207
Zymase, 172

281725 Bot M

Author Mottier, David Myers

Title A textbook of Botany.

University of Toronto Library

DO NOT REMOVE THE CARD FROM THIS POCKET

Acme Library Card Pocket
LOWE-MARTIN CO. LIMITED